University of Alberta

Internal and external controls over Holocene peatland development in Boreal western Canada

by

Ilka Elisabeth Bauer

©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Fall 2002

National Library of Canada
Acquisitions and Bibliographic Services
395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale du Canada
Acquisitions et services bibliographiques
395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-81163-8

Canada

University of Alberta

Library Release Form

Name of Author: Ilka Elisabeth Bauer

Title of Thesis: Internal and external controls over Holocene peatland development in Boreal western Canada

Degree: Doctor of Philosophy

Year this Degree Granted: 2002

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The Author reserves all other publication and other rights in association with the copyright in the thesis, and except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission

June 7, 2002

Vorderdeich 85
21037 Hamburg
Germany

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Internal and external controls over Holocene peatland development in Boreal western Canada* submitted by Ilka Elisabeth Bauer in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Environmental Biology and Ecology.

Dale H. Vitt, Supervisor

Mark R.T. Dale, Co-supervisor

L. Dennis Gignac, Committee member

Nathaniel W. Rutter, Committee member

Alwynne B. Beaudoin, Internal-external examiner

Pierre J.H. Richard, External Examiner

June 7, 2002

ABSTRACT

This thesis examines the developmental history of two large peatland complexes in boreal Alberta, and uses paleoecological analysis and simulation modelling to examine the applicability of established models of peatland development to continental peatlands.

At both Athabasca (55°03'N, 113°15'W) and Rainbow Lake (58°17'N 119°22'W) the earliest records of peat formation coincide with the end of early or mid-Holocene aridity, and early peat-forming communities were wet, monocot-dominated marshes or fens that occupied topographic depressions. At Athabasca, the speed and direction of lateral peat expansion were largely controlled by topography, although autogenically induced changes in drainage were important in promoting paludification. At both sites, basal paludified communities include monocot-dominated or woody rich fens and *Sphagnum*-dominated poor fens or bogs. Local successional pathways are diverse and point towards a continued influence of allogenic effects in peatland development. In peat plateau areas at Rainbow Lake, community change in the late Holocene reflects the effect of periodic fires and permafrost dynamics. At Athabasca, there is an overall tendency for succession of wet, minerotrophic communities to *Sphagnum*. However, topographically controlled differences in water flow have played an important role in controlling local community development.

Long-term (apparent) rates of peat accumulation are highly variable within each site. At Rainbow Lake, decreased accumulation during the late Holocene most likely reflects regional permafrost development. At Athabasca, peat buildup has been fastest in wet, minerotrophic fens and slowest in *Sphagnum*-dominated communities. A simulation model that examines effects of litter quality and environment on peat accumulation shows changes in the importance of individual parameters over time and suggests that dominant controls over peat accumulation differ between community types. Sudden changes in peat accumulation dynamics that follow environmental change are not necessarily detectable from cumulative mass / age profiles, and simple peat accumulation models may fit core profiles well even if several of their basic assumptions are violated. In order to increase the utility of paleoecological records in predicting peatland responses to climatic change, we need a more dynamic approach to the interpretation of paleoecological data.

CONTENTS

CHAPTER 1: INTRODUCTION

Autogenic Succession, the Clymo model, and peatland development in continental climates 1

INTRODUCTION 2

THE AUTOGENIC MODEL OF PEATLAND DEVELOPMENT 2

Early accounts 2

The early 20th century 3

Frederic Clements and the hydrosere model of vegetation succession 3

C.A. Weber and early Scandinavian studies 5

Characterization of wetland communities 6

Current evidence 7

Terrestrialization 8

(a) The limnic phase 8

(b) Telmatic communities 9

Paludification 12

Fen / bog transitions 15

The autogenic model - conclusions 16

THE CLYMO MODEL 18

Background 18

The model 18

Evidence and applicability 20

The Clymo model - conclusions and further developments 24

STRUCTURE OF THIS THESIS 25

LITERATURE CITED 27

CHAPTER 2: **Importance of climate and physiography in controlling succession and rates of peat accumulation in central Alberta** 43

INTRODUCTION 44

STUDY AREA 47

METHODS 49

Field sampling 49

Spatial analysis 50

physico-chemical analysis and ^{14}C dating 50

Macrofossil analysis 52

Statistical analysis of macrofossil data 52
Clustering and ordination 52
Core zonation 53
Environmental interpretation of successional trends 53
RESULTS 55
Peat depth interpolation 55
Core lithologies 55
Macrofossil analysis 56
Clustering and ordination 56
Inferred environmental change through time 57
Basal dates and rates of peat accumulation 59
INTERPRETATION 59
Local community succession 59
DISCUSSION 61
Peatland initiation and landscape succession 61
Before 7000 cal. BP 61
7000 - 5000 cal. BP 63
5000 - 3000 cal. BP 64
3000 cal. BP - present 65
Factors controlling peatland expansion 66
Patterns of vegetation succession 68
Vertical peat accumulation rates 68
LITERATURE CITED 70
TABLES 83
FIGURES 85

CHAPTER 3: **Peatland development in the discontinuous permafrost zone of northern Alberta** 100
INTRODUCTION 101
STUDY AREA 104
METHODS 106
Field sampling 106
Core sampling and description 107
Analysis of macrofossil data 108
Clustering and ordination 108
Charcoal content 109
Peat depth distribution 109

RESULTS 111
Peat depth distribution 111
Macrofossil stratigraphies 112
Fen and swamp cores 112
Peat plateau cores 113
deep cores 113
shallow cores 115
Clustering and ordination 116
Distribution of charcoal 117
Basal peat dates and rates of peat accumulation 117
INTERPRETATION 118
Patterns of community development 118
Clustering and ordination 120
DISCUSSION 121
Development of the Rainbow Lake site 121
Before 8000 cal. yrBP 121
8000 - 4000 cal. yr BP 123
4000 cal. yrBP - present 126
Efficacy of macrofossil data in paleoenvironmental reconstruction 127
Peat charcoal content 128
Long-term rates of peat accumulation 129
LITERATURE CITED 131
TABLES 142
FIGURES 145

CHAPTER 4: Modelling effects of litter quality and environment on organic matter accumulation over different timescales 162
INTRODUCTION 163
MODEL STRUCTURE 166
Net primary productivity (NPP) 167
Decay 169
Internal decay modifiers 169
Nitrogen content 170
Lignin-related variables 171
External decay modifiers 172
pH and oxygen availability 172
TESTING MODEL BEHAVIOUR 174

Sensitivity analysis 174
Static peatland types 174
Effects of community change 175
Inferred organic matter accumulation 175
RESULTS 176
Sensitivity analysis 176
Static peatland types 177
Effects of community change 178
Inferred organic matter accumulation 178
DISCUSSION 179
Model sensitivity and static peatland types 181
Effects of environmental change 183
Limitations of paleoecological data 184
LITERATURE CITED 186
TABLES 196
FIGURES 202

CHAPTER 5: Overall discussion and conclusion 214
RESULTS OF THIS THESIS AND THE AUTOGENIC MODEL 215
PATTERNS OF ORGANIC MATTER ACCUMULATION AND THE CLYMO MODEL ... 218
PEATLAND RESPONSE TO FUTURE CLIMATE CHANGE 220
CONCLUSION 220
LITERATURE CITED 222

APPENDIX 1: Relationships between landforms shown in Figures 2.2 and 3.3 and wetland types recognized by the Alberta Wetland Inventory Classification Standards 226

APPENDIX 2: Reference material used in macrofossil determination and concepts used for identification of important macrofossil taxa 228

APPENDIX 3: Macrofossil diagrams for Athabasca cores 3, 10, 16, 17 and 18 237

LIST OF TABLES

2.1 Minimum variance cluster groups for macrofossil data from Athabasca cores 3, 10, 16, 17 and 18, and taxa with significant indicator values for each cluster 83

2.2 Basal radiocarbon dates and long-term apparent rates of peat accumulation for Athabasca cores 84

3.1 Minimum variance cluster groups for macrofossil data from Rainbow Lake cores, and taxa with significant indicator values for each cluster .. 142

3.2 Univariate logistic regressions of CHARCOAL on depth, macrofossil groups, and NMDS axes 143

3.3 Variables used in the final logistic regression model for CHARCOAL 143

3.4 Basal radiocarbon dates and long-term apparent rates of peat accumulation for Rainbow Lake cores 144

4.1 Nitrogen content of different peat types assumed by the model 196

4.2 Parameters manipulated during sensitivity analysis 197

4.3 Parameterization for different litter types, surface decay rates, and external decay modifiers used in static simulations 198

4.4 Ability of different input parameters to increase peat accumulation over different timescales 199

4.5 Total NPP ($g \cdot m^{-2} \cdot yr^{-1}$), relative contribution of different vegetation types, and turnover rates (α, yr^{-1}) for static simulations 200

4.6 Parameter estimates for fitted Clymo-type models in dynamic simulations 201

A1.1 Mapped wetland types and corresponding landform designations used in Figure 2.2 (Athabasca) 227

A1.2 Mapped wetland types and corresponding landform designations used in Figure 3.3 (Rainbow Lake) 227

LIST OF FIGURES

1.1	Mechanisms of peatland initiation. (a) Terrestrialization; (b) Paludification	4
1.2	Structure and important parameters of the Clymo model	19
1.3	Hypothetical profiles of cumulative peat mass (above a given depth) and age of peat at that depth	21
1.4	Different ways to report peat accumulation rates, and their relative magnitude according to the Clymo model	21
2.1	(a) Location of the Athabasca site within Alberta, Canada, and (b) aerial photograph of the Athabasca peatland complex	85
2.2	Map of the Athabasca study area showing main peat landforms, depth survey points with valid measurements, and coring locations	86
2.3	Landform diversity at the Athabasca peatland complex.:(a) the open fen area; (b) the northern bog	87
2.4	(a) The Macaulay peat sampler; (b) basal section of peat core.	88
2.5	Anisotropic variogram model used for spatial interpolation of trend surface residuals at Athabasca	89
2.6	Classification used to assign samples to broad peat type categories	90
2.7	Interpolated map of peat depth throughout the Athabasca study area	91
2.8	Lithology of 16 cores from the Athabasca site	92
2.9	Overall successional development in 16 cores from the Athabasca site ..	93
2.10	DCA ordination of 136 macrofossil samples from Athabasca cores 3, 10, 16, 17 and 18	94
2.11	Mean indicator values and tolerance ranges of macrofossil taxa for depth to water table, pH, and conductivity corrected for hydrogen ions	95
2.12	(a) Directions of maximum change in environmental variables within the Athabasca macrofossil ordination, and (b-f) successional trajectories of cores 3, 10, 16, 17 and 18 in ordination space	96
2.13	Relationship between basal peat age and present peat depth in Athabasca cores	97
2.14	Relationships between long-term rates of peat accumulation and average scores for (a) *Sphagnum* and (b) herbaceous material in Athabasca cores	98
2.15	Pattern of peat expansion over time at the Athabasca site, as inferred	

	from basal peat dates	99
3.1	(a) Location of the Rainbow Lake site within Alberta, Canada, and (b) aerial photograph of the Rainbow Lake peatland complex	145
3.2	Appearance of the former peat plateau regions at Rainbow Lake in 1996 .	146
3.3	Map of the Rainbow lake site showing main peat landforms, depth survey points, and coring locations	147
3.4	Relationship between field measurements of peat depth (probe depth) and basal depth (20% ash limit) at coring locations	148
3.5	Differences in basal depth between landform types at Rainbow Lake	149
3.6	Sample variograms and fitted exponential models for the Rainbow Lake site at 10 successive indicator thresholds	150
3.7	(a) Mean peat depth prediction for each grid node from 500 realizations, and (b-f) five of the 500 realizations generated by stochastic simulation for the Rainbow Lake site	151
3.8	Macrofossil diagrams for three fen cores (a, b and d) and a treed swamp (c) at the Rainbow Lake peatland	153
3.9	Macrofossil diagram for a poor fen core from the Rainbow Lake site	154
3.10	Macrofossil diagram for a deep peat plateau core (no. 8) from the Rainbow Lake site	155
3.11	Macrofossil diagram for a deep peat plateau core (no. 10) from the Rainbow Lake site	156
3.12	Macrofossil diagram for a deep peat plateau core (no. 3) from the Rainbow Lake site	157
3.13	Macrofossil diagrams for three shallow peat plateau cores from the Rainbow Lake site	158
3.14	NMDS ordination of Rainbow Lake macrofossil data. (a) Axis 1 and axis 2; (b) axis 1 and axis 3	159
3.15	Changes in charcoal content with depth in 173 macrofossil samples from Rainbow Lake	160
3.16	(a) Relationship between basal peat age and depth at Rainbow Lake, and (b) plot of long-term apparent rates of peat accumulation ($mm \cdot yr^{-1}$) against basal age	161
4.11	Partitioning of organic matter within the peat column	202
4.2	Relationship between weight of overlying material and the bulk density of different litter types. (a) bryophyte and *Sphagnum* peat ; (b) woody and herbaceous peat	203

4.3 Aboveground NPP of different vegetation components as a function of pH and water table depth. (a) herbaceous; (b) wood; (c) non-*Sphagnum* bryophytes; (d) *Sphagnum* 204

4.4 (a) Aboveground, and (b) total NPP as a function of pH and water table depth 205

4.5 Vertical distribution of (a) herbaceous and (b) woody belowground NPP assumed by the model 206

4.6 Overview over adjustments made to user-specified surface turnover rates for the three chemical fractions recognized by the model 207

4.7 Changes in the temperature modifier (Zt) with depth 208

4.8 (a) Relationship between mean water table depth and the range of (annual) fluctuations assumed by the model; (b) proportion of time a cohort spends above the water table 209

4.9 Mass accumulation by different scenarios tested during sensitivity analysis 210

4.10 Changes in peat mass over time in simulations with static water table and pH 211

4.11 Effect of community transition on (a & b) mass accumulation over time, and (c & d) the relationship between cohort age and cumulative mass in final core profiles 212

4.12 Difference between actual (net) rates of organic matter accumulation and rates inferred from core profiles. (a) apparent rates; (b) rates corrected for decay by fitting Clymo-type accumulation models 213

A3.1 Macrofossil diagram for Athabasca core 3 (fen edge) 238

A3.2 Macrofossil diagram for Athabasca core 10 (western bog) 239

A3.3 Macrofossil diagram for Athabasca core 16 (northern bog) 240

A3.4 Macrofossil diagram for Athabasca core 17 (open fen) 241

A3.5 Macrofossil diagram for Athabasca core 18 (treed fen) 242

List of Symbols and Abbreviations

General

$\delta^{13}C$	The ratio of stable carbon isotopes (^{13}C : ^{12}C) relative to the PDB standard
ANOVA	Analysis of variance
AVI	Alberta Vegetation Inventory
BGS	Identifier for the radiocarbon laboratory at Brock University, Geoscience Department
cal. yr BP	Years before present (calibrated radiocarbon years)
cdf	Cumulative distribution function
DCA	Detrended correspondence analysis
GSC	Geological Survey of Canada
IV	Indicator value of a taxon (in a macrofossil cluster group)
K_{corr}	Conductivity corrected for hydrogen ions
ln or $\log_e$	Natural log
NMDS	Non-metric multidimensional scaling
NPP	Net primary productivity
PDM	Peat Decomposition Model (Frolking *et al.* 2001)
r	A correlation coefficient
R^2	Coefficient of determination
RA	Relative abundance
RF	Relative frequency
SD or σ	Standard deviation
SE	Standard error
TSAI	Thermal seasonal aridity index
yr BP	Radiocarbon years before present
ZPD	Zoltai Peatland Dataset (Zoltai *et al.* 2000)

CHAPTER 1

α	Exponential decay coefficient
α_a	acrotelm decay coefficient
α_c	catotelm decay coefficient
m	Organic matter mass
m_0	Initial organic matter mass
p_a	Acrotelm productivity
p_c	Catotelm productivity
t	Time

CHAPTER 2

i	Subscript referring to a sample
j	Subscript referring to a taxon
k	Subscript referring to a cluster
$\hat{t}$	Inferred tolerance range (weighted standard deviation)
$\hat{u}$	Indicator value (of a taxon for an environmental variable) inferred by weighted averaging
x	Measured value of an environmental variable
$\hat{x}$	Inferred value of an environmental variable
y	Abundance

CHAPTER 3

-2LL	Model deviance
BBRYO	Presence / absence of *Pohlia*, *Polytrichum* or *Mylia anomala* in a sample
CHARCOAL	Presence / absence of ≥ 2% charcoal in a macrofossil sample
G	Log likelihood ratio
G_M	Model chi-square or goodness of fit
HERB	Proportion of sample made up of herbaceous remains
LICHEN	Presence / absence of lichens in a sample
OBRYO	Presence / absence of bryophytes (other than *Sphagnum* and those

	contained in BBRYO) in a sample
SPHA	Proportion of sample made up of *Sphagnum* section Acutifolia
SPHC	Proportion of sample made up of *Sphagnum* section Cuspidata
Wald	Wald statistic
WOODY	Proportion of sample made up of woody plant remains

CHAPTER 4

α	Turnover rate
α_{Ac}	Actual (final) turnover rate after application of all internal and external decay modifiers
α_{Lq}	Turnover rate after application of all internal (litter-quality dependent) decay modifiers
α_{Nc}	Turnover rate after correction for litter nitrogen content
α_{Sf}	User-specified maximum surface turnover rate
β	Proportion of time spent above the water table
ϕ	Amplitude of annual water table fluctuations (cm)
π	pH-dependent decay multiplier; a component of Zoa
θ	Nitrogen factor
ρ	Ratio of anoxic : oxic organic matter turnover at a given pH level; a component of Zoa
ω	Mean annual water table position (cm below the peat surface)
coh	Subscript referring to a cohort
d	Distance (in lattice coordinates)
f	Subscript referring to a chemical fraction
HOL	Holocellulose
i	Subscript referring to a year
j	Subscript referring to a (root) generation
k	Subscript referring to a litter type
LIG	'Lignin' - the acid-insoluble fraction of organic matter characterization
M	Mass
M_0	Original mass

NPP_{bg}	Belowground NPP
NPP_{total}	Total NPP
p	Rate of mass input
p	Subscript referring to a data point in environmental space
q	Subscript referring to a point in environmental space at which prediction is required
Q	Lignocellulose quotient
Q_0	Lignocellulose quotient of fresh, easily decomposable litter
Q_c	Value of Q at which HOL decays at the same rate as LIG ('asymptotic' lignocellulose quotient)
r	Search radius (in lattice coordinates)
S	Maximum re-scaled value for pH and water table depth (lattice coordinates).
SOL	The soluble organic matter fraction
T	Time
w	Weight assigned to a data point
Za	Value of Zoa under fully anoxic conditions
Zo	Value of Zoa under fully oxic conditions
Zoa	A pH-dependent oxic : anoxic decay modifier
Zt	The temperature modifier

CHAPTER 1: INTRODUCTION

Autogenic succession, the Clymo model, and peatland development in continental climates

INTRODUCTION

Peatlands are wetland ecosystems that accumulate dead organic material in the form of peat. Much of our present conceptual framework for understanding peatland development is based on the study of raised bogs in oceanic and sub-oceanic regions of Europe. The majority of the world's peatlands, however, are located in continental areas of Eurasia and North America (Gorham 1991). The present geographic distribution of peatland types suggests strong climatic control over peatland development (Eurola 1962; Moore and Bellamy 1974; Glaser and Janssens 1986). The cold, dry climate of continental regions offers an opportunity to examine peatland dynamics within a new framework, and to critically examine the general applicability of paradigms developed in more oceanic regions. This thesis will focus on two of these 'paradigms': the autogenic model of vegetation succession, and the Clymo (1984a) model of peat accumulation. The aim of this chapter is to provide an overview of the development of the models, and to review some of the evidence for their applicability, with specific focus on continental peatlands. Questions related to the climatic interpretation of stratigraphic sequences, in particular the problem of recurrence surfaces, will not be discussed. See Korhola (1992; p. 82-84) for a brief introduction to the extensive literature on the subject.

THE AUTOGENIC MODEL OF PEATLAND DEVELOPMENT

Begon *et al.* (1990) define **autogenic successions** *as 'successions that occur as a result of biological processes* (...) *that modify conditions and resources'*. **Allogenic successions**, on the other hand, occur *'as a result of external geophysico-chemical forces'*. More generally, the term **autogenic factors** will be used in the following to refer to changes or processes that are a result of *in situ* biological activity, whereas the term **allogenic factors** refers to abiotic influences that arise externally to the peatland.

Early accounts

The notion that peatlands are formed through the gradual filling of water bodies by vegetation (**terrestrialization**) originated several centuries ago. King (1685)

described a sequence of vegetation types leading from wet fen to bog. By the early 19th century, authors such as Aiton (1811) had described community types involved in terrestrialization and realized that their temporal succession resulted from the accumulation of dead plant material and consequent elevation of living vegetation above the level of the original lake. Thus, the autogenic nature of the process was understood two hundred years ago, as was the fact that terrestrialization sequences are often reflected both in the stratigraphy of peat deposits and in the zonation of vegetation around existing lakes. These early authors further realized that not all peatlands originate as lakes. King (1685) described the spread of bog into formerly arable areas of Ireland during historic times, and several authors noted the ubiquity of tree remains at the base of English and Scottish blanket peats. Aiton (1811) attributed the spread of blanket peat to felling of trees that began in Roman times, whereas Geikie (1865) believed that the replacement of forest by peatland was a result of climatic deterioration and began long before the Romans arrived in Britain.

In a review of early ideas concerning peatland development, Gorham (1953) noted that professional ecologists have mostly failed to recognize these early peatland studies. Consequently, the development of ecology as a discipline in the early 20th century has often involved the re-discovery of ideas that had been proposed long previously, albeit within a new theoretical framework and using new methodologies.

The early 20th century

Frederic Clements and the hydrosere model of vegetation succession

Many early ecologists who studied causes and mechanisms of plant succession were interested in peatland development. Clements (1916) used the in-filling of lakes as a key example in his treatment of plant succession. He coined the term **hydrosere** to describe a successional sequence that begins under wet conditions (p. 182). According to the organismic view of vegetation development proposed by Clements (1916) peatland communities are transitory, representing mere seral stages in the development towards a final climax of mesophytic forest. Support for this notion was

largely based on the observable zonation of vegetation around lakes. According to Clements (1916), 'zonation is the epitome of succession'. Because of this view, the concept of a mesophytic forest climax has pervaded the ecological literature for much of the 20th century (see Klinger 1996b), although it was questioned soon after its first proposal. Pearsall (1918) regarded peatlands as the endpoint of hydrosere succession in the English Lake district. This view was later adopted by Godwin and Turner (1933) and Tansley (1939) for most of the British Isles, although they did believe that succession to oak forest was possible in sub-oceanic regions (see Tansley 1939 p. 671). Walker (1970) finally rejected this notion based on an extensive review of data from British post-glacial hydroseres.

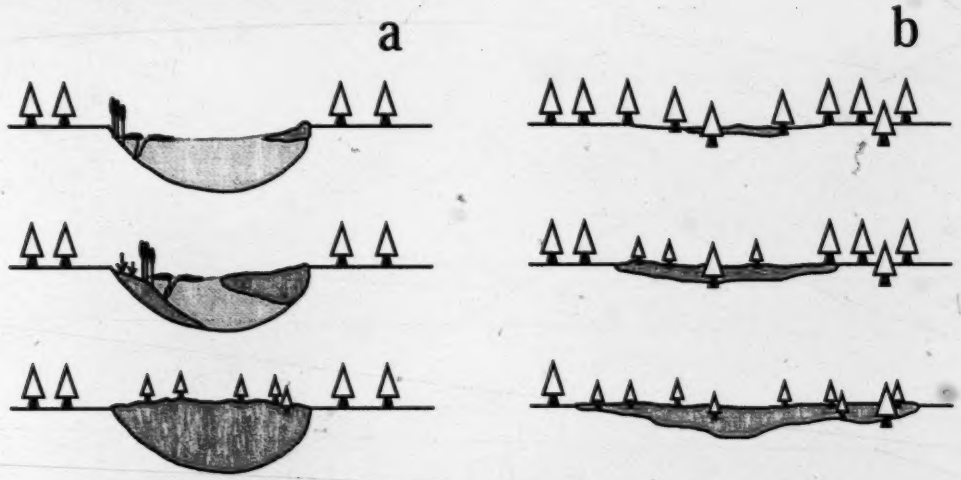


Figure 1.1: Mechanisms of peatland initiation. **(a)** Terrestrialization. This involves the gradual in-filling of a lake basin with organic remains, with peat eventually building up above the level of the original water table. Terrestrialization can proceed either by centripetal encroachment of rooted macrophytes (left) or through formation of a floating vegetation mat (right). **(b)** Paludification. Upland (forest) is replaced by peatland, without an intervening lake phase.

Clements (1916) regarded vegetation succession as inherently directional, with both hydrarch and xerarch sequences ultimately leading to a mesophytic forest climax. Within this framework, **paludification** (the conversion of upland forest to peatland; Figure 1.1) is regressive, and Clements did not believe it occured in the absence of external disturbance such as flooding, forest clearance or climate change (1916; p.

145-167). He rejected the notion that natural soil change in upland forest can facilitate the establishment of 'lower' vegetation types (1916; p. 162). Presumably because of the inaccessibility of the vast boreal peatland areas of Canada, and perhaps to some degree owing to the continued influence of Clements's ideas, few North American studies have tried to characterize or quantify paludification until the end of the 20th century.

C.A. Weber and early Scandinavian studies

In Scandinavia and Germany, models of peatland development have always been based on stratigraphy, and the idea that peatlands give rise to mesic upland forest was apparently not seriously considered. Based on extensive studies of peatlands in northern Germany, Weber (1908) described a generalized sequence of community types that replace one another in a largely predictable order, culminating in raised bog: Basal **limnic** communities are made up of submerged and floating vegetation and produce gyttja and dy deposits. **Gyttja** is largely autochtonous and contains remains of microscopic organisms and inorganic sediment. **Detritus gyttja** further contains macroscopic remains of aquatic plants. **Dy** is gyttja mixed with acid humus. It is largely allochtonous and characteristic of acidic lakes. (see Hansen 1959; Spence 1964 p. 314-16; Wetzel 1983; Succow and Jeschke 1990).

After sufficient sediment accumulation, limnic communities are replaced by **telmatic** communities composed of emergent taxa such as *Phragmites* and different *Carex* spp. As peat buildup continues, telmatic communities are invaded by brown mosses such as *Hypnum* spp. and *Scorpidium,* initiating transition to **semi-terrestrial** communities. In northern Germany, semi-terrestrial communities are mainly represented by alder carr (*Erlenbruchwald*) and produce woody peat deposits. Continued peat buildup eventually leads to the origin of **terrestrial** communities, initially dominated by *Pinus* and *Betula* and later invaded by *Sphagnum* and taxa characteristic of raised bog. According to Weber (1908) this successional sequence is

associated with a change in nutrient status from eutrophic during the limnic phase to oligotrophic in the final raised bog.

Like Clements (1916), Weber (1908) believed that the progression from lake to raised bog is an autogenic process. Unlike his North American colleague, however, Weber (1908) recognized that peat often initiates in forested environments.

During the first half of the 20th century, these views were expanded by extensive Scandinavian studies. Classifications developed by workers such as Cajander (1913) and Aario (1932) included both true peatland communities and transitional forest types, thus acknowledging that paludification is an important mechanism of landscape development in boreal regions. Extensive stratigraphic studies of Scandinavian peat deposits soon demonstrated that lake terrestrialization is a common means of peatland initiation. However, they also showed that most of the current boreal peatland area is not underlain by lake deposits. Workers such as Kujala (1924), Aario (1932) and Huikari (1956) estimated that about 95% of all Finnish peat deposits originated either through paludification or **primary mire formation** (i.e. peat initiation on newly exposed land, usually in coastal areas following isostatic uplift). The potential impact of continued paludification on forestry operations soon prompted investigations into mechanisms of paludification (Cajander 1913; Aario 1932; Malmström 1932), and into the possibility of its occurrence in modern times (Malmström 1932; Lukkala 1933). Although mainly descriptive, these studies laid the basis for almost all modern theories of forest / peatland interaction.

Characterization of Wetland communities

In the early 20th century, environmental differences between wetland communities were increasingly well quantified. Pearsall (1917; 1918; 1920), Wilson (1935) and Jewell and Brown (1929) examined the distribution of aquatic communities in relation to factors such as water chemistry, depth and sediment characteristics. Godwin and Bharucha (1932) provided detailed records of water table fluctuations in Wicken fen and their control of plant communities, and authors such as

Sjörs (1950b) described vegetation zonation in relation to water table depth in the peatlands of Scandinavia. The influence of chemical gradients such as pH and conductivity on peatland vegetation was investigated by Kurz (1928), Godwin and Turner (1933), Conway (1949) and Sjörs (1950a). The fact that *Sphagnum* and some other mosses are the cause of peatland acidity, rather than just colonizers of acidic habitats, was recognized very early (Kurz 1928), establishing *Sphagnum* as a key player in the autogenic model of vegetation succession. A distinction between rain-fed and other peatland types (i.e. **ombrogenous** vs. **geogenous** systems) was recognized by authors such as Weber (1908), Steffen (1931) and Tansley (1939), as was the dependence of true 'raised' bog on climate (e.g. Ganong 1897; Granlund 1932). Use of the mineral soil water limit (Thunmark 1940), as identified by floristic criteria, to delineate these main groups was advocated by du Rietz (1949), who coined the terms **ombrotrophic** and **minerotrophic** to denote associated differences in mineral status (du Rietz 1954). Although the utility of these terms has been questioned by recent reviews (Bridgham *et al.* 1996; Wheeler and Proctor 2000), their use is usually implied in the classification of peatlands into bogs and fens.

Current evidence

All available evidence indicates that both terrestrialization and paludification are common processes. In terms of the autogenic hypothesis, two questions have to be considered at this point: (a) What triggers these different means of peatland initiation? and (b) Once peat accumulation has begun, is subsequent development largely under autogenic control? The relative importance of autogenic versus allogenic factors as driving mechanisms of peatland evolution has been discussed previously (e.g. Sjörs 1980; Tallis 1983; Payette 1988; Kuhry *et al.* 1993), and it is impossible to give a full review of the debate here. Rather, focus will be on the importance of different forcing mechanisms during peat initiation, and the continued influence of allogenic factors once peat accumulation is under way.

Terrestrialization

(a) The limnic phase

Adopting Weber's (1908) classification, limnic communities are here defined as dominated by submerged and floating macrophytes or by phytoplankton. Under the Canadian system of wetland classification (Tarnocai *et al.* 1988; Zoltai 1988) these would mostly fall into the shallow open water category. If terrestrialization is initiated by development of a floating mat, taxa involved are usually characteristic of fen environments. This type of terrestrialization will be discussed in a later section.

The ability of submerged vegetation to become established in a lake depends on a number of mutually interacting factors (Spence 1982). In his classic studies of lakes and their associated vegetation in the English Lake District, Pearsall (1917; 1920; 1921) identified rates of inorganic silt deposition and substrate characteristics (texture and organic matter content) as the main factors controlling macrophyte distributions. He remarked on the dependence of these variables on physical characteristics of the lake basin such as shape and size, and on differential exposure of shorelines. Spence (1982) reviewed these relationships, as well as their effect on nutrient availability. In general, aquatic vegetation is associated with sheltered bays and fine-grained substrates that not only allow rooted macrophytes to become established but also increase nutrient availability. Because of the low critical erosion velocity of organic matter, its *in situ* accumulation is only possible in extremely sheltered bays or in small lakes with little wave action (Spence 1982). The vertical distribution of macrophytes is mainly limited by light availability (Spence 1982), and steep-sided lake basins are less likely to terrestrialize (Tikkanen and Korhola 1993). In deeper lakes, hydroseral sequences may only be initiated after thick layers of inorganic sediment or algal gyttja (*Lebermudden*) have accumulated (Succow and Jeschke 1990; Bunting and Warner 1998). The accumulation of **sapropel** (neutral humus; *Faulschlamm*) under anaerobic reducing conditions in highly eutrophic, stagnant water bodies may produce the same effect (Steffen 1931; Succow and Jeschke 1990).

Rooted macrophytes acquire nutrients mainly from sediments (Carignan and Kalf 1980; Spence 1982), and their distribution is thus dependent on sediment characteristics more than water chemistry. In practice, these factors are usually linked, and nutrient-rich lakes have the potential to terrestrialize faster than those that are nutrient-poor (Succow and Jeschke 1990). Trophic status also plays a role in determining the most likely type of hydroseral sequence, with oligotrophic lakes and mesotrophic acidic lakes generally terrestrializing through formation of a floating mat (*Schwingmoor*) rather than the buildup of remains from rooted macrophytes. (Kulczynski 1949; Steffen 1931; Succow and Jeschke 1990).

In order for terrestrialization to proceed, water levels have to decrease relative to those of the sediment in which plants are rooted. While this is generally regarded as being the result of autogenic sediment (peat) accumulation (Weber 1908; Clements 1916; Walker 1970), many authors have noted the likely role of allogenic factors in accelerating the process. Pearsall (1918; 1920; 1921) and Spence (1964; 1982) observed rapid hydroseral development in areas of fast inorganic sediment accumulation, and Succow and Jeschke (1990) regard many cases of terrestrialization as induced by reduced water levels resulting from human activity. In an analysis of Holocene lake and peat sequences from Ontario, Bunting and Warner (1998) observed a sudden transition from shallow open water to terrestrial communities at several localities about 8000 BP, corresponding to a period of maximum climatic dryness. Tikkanen and Korhola (1993) documented rapid conversion of open water to reed swamp in a small hilltop basin at about 6000 BP, concurrent with lowered lake levels throughout southern Finland and Sweden.

(b) Telmatic communities

Weber (1908) defined telmatic communities (*Sumpfpflanzenvereine*) as dominated by emergent taxa such as *Phragmites*, *Scirpus*, *Typha*, and some *Equisetum* and *Carex* spp. Functionally, the term telmatic refers to peat *formation 'at the water table due to plants growing under conditions of periodic flooding'* (Gore 1983). Although widely used in Europe (e.g. Aario 1932 p. 108; Kulczynski 1949; Tallis

1983; Korhola 1992) the term does not seem to be well established in the North American literature. Taxa associated with telmatic communities come from a variety of different wetland types, including marshes and both rich and poor fen. Within a given phytogeographic region, community composition depends on (a) water chemistry (Kulczynski 1949; Conway 1949; Vitt and Slack 1975; Succow and Jeschke 1990; van Wirdum *et al.* 1992), and (b) the type of terrestrialization sequence. Lake infilling can result from the centripetal encroachment of emergent vegetation (**infraaquatic** terrestrialization) or floating mat formation (**supraaquatic** terrestrialization; *Schwingmoorverlandung;* e.g. Cajander 1913; Jewell and Brown 1929; Tallis 1983; Succow and Jeschke 1990). The transition between telmatic and terrestrial communities is gradual, at least floristically. Species that are sensitive to water level fluctuations or inundation may occur in telmatic communities if buffered by growth on a floating mat or buoyant peat matrix. (See Kulczynski 1949 p. 294-307). In the present context, the term 'telmatic' carries no implication as to pH, base or nutrient status. It is a purely functional term that refers to communities at the interface between truly aquatic and terrestrial habitats.

Under natural conditions, eutrophic water bodies sustain more productive macrophyte communities and are more likely to be through-flow systems with current velocities that prohibit mat formation (Kulczynski 1949). Consequently, eutrophic lakes are more likely to terrestrialize infraaquatically (Kulczynski 1949; Steffen 1931; Succow and Jeschke 1990). Much of what was said in the previous section about effects of lake morphology on the establishment and growth of aquatic macrophytes applies to telmatic communities that are rooted in the lake bottom. In Britain and Central Europe, these infraaquatic communities are generally dominated by *Phragmites*, which forms extensive areas of reedswamp in suitable locations (Kulczynski 1949; Tallis 1983). In Scandinavia and North America, large *Carex* spp and taxa such as *Equisetum fluviatile* and *Typha* assume greater importance (Dachnowski 1912; Cajander 1913; Tallis 1983). Many of these large emergent taxa

can also form floating mats, and lake terrestrialization often involves both supra- and infraaquatic communities.

Factors that induce mat formation seem to be variable and poorly understood. Wilcox and Simonin (1988) consider steep-sided clay-lined basins that are deep and lack in- and outflows as most conducive to rapid mat formation. Not all sites, however, fit this description, and other factors such as increased runoff following regional deforestation for agriculture (Warner *et al.* 1989) or changes in lake water levels (Tallis 1973; Wilcox and Simonin 1988) may contribute to mat formation. Once initiated, floating mats can rapidly overgrow small basins, as evidenced by names like *mere* or *llyn* (both meaning 'lake') for some small British mires (Tallis 1973; Moore and Beckett 1971) and observed rates of succession in Dutch peat cuttings (Bakker *et al.* 1994). Buell *et al.* (1968), on the other hand, observed no change in the extent of a floating mat over 33 years, and attributed this to continual erosion of peat at the mat edge. Cajander (1913) believed that erosion by wind and currents in many cases exceeds the rate of mat growth, thus limiting supraaquatic terrestrialization to extremely sheltered situations.

The initial floristic composition of floating mat communities depends on lake water chemistry. In water of low pH and alkalinity poor fen species are well represented, whereas pioneer mats on alkaline lakes are dominated by rich fen taxa such as *Sphagnum teres* and *S. subsecundum* or brown mosses of the Amblystegiaceae (Cajander 1913; Vitt and Slack 1975). A structural template for the growth of these species is provided by interwoven roots and branches of woody taxa such as *Myrica gale* and *Chamaedaphne calyculata* (Swan and Gill 1970; Kratz and deWitt 1986) or by herbaceous rhizomes of *Carex* spp., *Eriophorum, Phragmites* and *Typha* (Kulczynski 1949; Conway 1949; Tallis 1973). In exposed situations or when water tables are unstable, the bryophyte layer is often poorly developed (van Wirdum *et al.* 1992). While the lake basin is gradually filled by sedimentation from the mat bottom, vegetation development on top of the mat proceeds independently, sometimes

resulting in sizable peat deposits suspended over several metres of water (Moore and Beckett 1971; Green and Pearson 1977; Wilcox and Simonin 1988).

Paludification

Communities at paludifying sites are comprised of a mixture of forest and wetland species, the latter often including taxa characteristic of non-peat-accumulating wetlands (Korpela and Rainikainen 1996). Exact community composition depends on the amount of available water and on the nutrient status of the underlying soil. The amount and chemical composition of water, in turn, depend on the type of hydrological change that triggers paludification and on substrate permeability (Aario 1932). Basal peats of paludified sites can be woody, herbaceous or *Sphagnum*-dominated, or comprise a mixture of these basic types (e.g. Aario 1932; Tolonen 1967; Korhola 1992).

Malmström (1932) described three main mechanisms that can trigger paludification in northern Sweden: flooding (*Überschwemmung*), exposure to runoff (*Überrieselung*) and increase in local or regional groundwater levels. Deposition of limnic peat close to lake outflows can impede drainage and cause flooding around lake margins (Malmström 1932). Several instances of localized flooding and consequent peatland initiation, or changes in peat accumulation dynamics, have been attributed to the activity of beaver (McIntyre *et al.* 1991; Bhiry 1996, Wells *et al.* 2000). Depending on the severity of flooding, communities resulting from this type of 'paludification' can be representative of lake, marsh, swamp or fen communities.

Paludification caused by runoff is usually attributed to water draining from existing peatlands (Auer 1921; Malmström 1932). Aario (1932) regarded this process as the most important form of paludification in his study area in western Finland. The speed at which peat can spread from initial nucleation areas depends on the amount of runoff, substrate slopes, and the permeability of the underlying soil. Runoff from peatlands on flat substrates of low hydraulic conductivity can rapidly paludify relatively large areas, whereas sloping margins or permeable substrates retard lateral

expansion (Malmström 1932; Ivanov 1981). Once peat accumulation has begun within a basin, the deposition of humified organic matter can clog soil pores and reduce permeability of the underlying substrate, leading to increased runoff at the peatland margins and lateral peat expansion (Futyma and Miller 1986; Miller and Futyma 1987; Almquist-Jacobson and Foster 1995). This type of paludification is probably linked to vertical peat accumulation, because water levels have to rise in order for the peatland to drain onto new mineral terrain (Auer 1921).

Community composition at the paludifying edge depends on the type of peatland that supplies runoff and on soil composition. In southwestern Finland, raised bog expanding into nutrient-poor mineral terrain involves replacement of feather mosses by *Polytrichum commune* and *Sphagnum girgensohnii*. These are succeeded by weakly mesotrophic species of the recurvum complex and, eventually, *S. acutifolium* (= *S. capillifolium*) and *S. fuscum* (Aario 1932). Paludification of richer soils is generally characterized by greater dominance of herbaceous taxa (Cajander 1913).

Malmström (1932) lists three mechanisms that can raise local or regional water tables and thus initiate paludification: loss of tree cover (after forest clearance or fire), climate change, and impeded drainage resulting from natural soil changes. Loss of tree cover results in decreased transpiration and a temporary rise in local water tables (Korhola 1992; 1995). Many paludified sites contain charcoal in their basal peat deposits, thus supporting a link between fire and paludification (e.g. Lukkala 1933; K. Tolonen 1967; M. Tolonen 1987; Kubiw *et al.* 1989; Korhola 1992). However, given the ubiquity of charcoal in boreal soils, the presence of charcoal alone is no proof that paludification was a direct result of fire (Cajander 1913; Filion and Bégin 1998). Human forest clearance is one of several factors that have been linked to the spread of blanket bog in Britain and Norway (e.g. Moore 1973; Solem 1989; Tallis 1991), and several authors have warned against indiscriminate logging in Canadian forest types that are vulnerable to peat- or heathland invasion (Wilde *et al.* 1954; Mallik 1995).

Climate change, soil development, and the establishment of key colonizing species are tightly linked in their ability to trigger forest - peatland succession. Direct

effects of climate are usually impossible to ascertain because development of a cooler, moisture climate triggers soil and vegetation changes that may have more direct (and more easily detectable) impacts on peat initiation. Soil and vegetation change, in turn, are interdependent, and it is hard to resolve which follows from the other.

Forest-peatland succession in Alaska is associated with podzolization and the formation of impermeable (placic) soil horizons (Ugolini and Mann 1979; Klinger 1996a). Because of its biochemical properties, *Sphagnum* (and to a lesser extent other bryophytes) may play a key role in accelerating this process. Exchange of hydrogen ions for inorganic cations by living plants and liberation of organic acids during decomposition both contribute towards the acidifying effect of *Sphagnum* (Clymo 1964; Hemond 1980; Clymo 1984b). Iron and aluminium are mobilized at low pH and form organometallic complexes that are translocated with percolating water. Precipitation of these complexes in lower soil horizons leads to the formation of placic horizons that reduce permeability to water or plant roots (Klinger 1996a).

Development of *Sphagnum* cover on forest soil has been linked to nutrient deficiency in black spruce (Heilman 1966; 1968), reduced soil aeration (Zobel 1990) and increased mortality of fine roots (Klinger 1990). Once established, *Sphagnum* mats can expand rapidly at the expense of other bryophytes (Noble *et al.* 1984; Foster 1984). *Sphagnum* is resistant to decomposition, both due to poor litter quality and the production of phenolic compounds that have antimicrobial properties (Johnson and Damman 1993; van Breemen 1995; Verhoeven and Toth 1995; Belyea 1996). In spite of this, *Sphagnum* establishment often does not lead to accumulation of deep organic deposits (Neiland 1971). Thus, although we have a good understanding of factors likely to contribute towards paludification, their mutual interdependence and interactions with climate and local site hydrology limit our ability to predict paludification patterns and carbon dynamics at the forest / peatland interface.

Fen / bog transitions

From the perspective of regional groundwater dynamics, fens develop in discharge areas, i.e. they receive water input from either overland flow or groundwater discharge. The water table of fens is at or below the local groundwater level, and they have concave or horizontal profiles in cross-section (Heinselman 1970; Ivanov 1981). Given favourable hydrotopographic conditions, fens can develop in areas that are too dry to sustain bogs (Ivanov 1981; Halsey *et al.* 1998). Bogs, according to the classic hydrological definition, act as groundwater recharge or throughflow systems. All bogs are 'raised' in the sense that their surface is isolated from the direct influence of mineral groundwater. In dry, continental areas, however, bog surfaces are only slightly elevated above the level of surrounding fens (Zoltai *et al.* 1988). The often markedly convex water table of oceanic raised bogs is maintained by high precipitation and poor permeability of peat in the catotelm, resulting in the formation of a groundwater mound (Ivanov 1981, Clymo 1984a). Raised bogs are therefore maintained by a dynamic equilibrium between water input and seepage.

Ombrotrophication is generally thought to result from buildup of peat above the mineral groundwater table, i.e. to be under autogenic control. However, in the first detailed study of continental peatlands, Kulczynski (1949) stressed the continued importance of allogenic factors in controlling fen / bog transitions. In continental regions of Europe and North America, fens cover large areas of land with gentle topographic gradients. Bogs form in specific physiographic settings such as drainage divides (Kulczynski 1949; Heinselman 1963; Glaser *et al.* 1997) and flat interfluvial areas (Glaser *et al.* 1997). Alternatively, they may initiate as ovoid bog islands within large fens, either over areas of slightly elevated mineral terrain or in local stagnation zones (Zoltai and Johnson 1985; Glaser 1987). Under these conditions, the isolation of vegetation from mineral groundwater is largely a result of physiographic position, not a regional climatic effect. Kulczynski (1949) further documented several cases where bog formation resulted from sudden changes in drainage patterns that were not a direct result of local peat accumulation.

Given the smaller atmospheric moisture surplus, complete ombrotrophication should occur less readily in continental than in oceanic climates. This is supported by the observation that continental fens occupy physiographic settings that characteristically support bog vegetation in more oceanic climates (Kulczynski 1949), and by the high abundance of fens in regions such as continental western Canada (Vitt *et al.* 1996; Halsey *et al.* 1997). Recent studies further suggest that continental bogs may not be as independent of their surroundings as suggested by classic definitions of fen versus bog. Hydrologic head measurements from bogs in the Glacial Lake Agassiz peatlands indicate that water moves upwards through the peat at some times (Siegel and Glaser 1987; Romanowicz *et al.* 1993, Glaser *et al.* 1997). Temporary changes in directions of groundwater flow have been documented from peatlands in New York (Drexler *et al.* 1999), Ontario (Devito *et al.* 1997) and northern Sweden (Devito *et al.* 1997; Waddington and Roulet 1997). While the sites examined included a variety of peatland types, these studies show that water movement in peatlands is variable both temporally and spatially, thus challenging the rigid views of peatland hydrology embedded in traditional definitions.

The autogenic model - conclusions

Depending on circumstances, peatland initiation (by terrestrialization or paludification) can represent either autogenic or allogenic succession. A shallow, sheltered lake basin may start to terrestrialize purely autogenically. Frequently, however, the establishment of aquatic macrophytes is initiated or accelerated by allogenic factors such as water level changes or inorganic sedimentation. If paludification is a result of reduced soil permeability, it may be an autogenic process that follows from local soil development. Paludification that is triggered by flooding, fire or climate change, on the other hand, represents allogenic succession. In many cases, particularly when peat initiation is triggered by expansion of neighbouring peatlands, distinction between autogenic and allogenic influences may be difficult and both are likely to contribute towards peat initiation.

Once peat has initiated at a site, autogenic factors undoubtedly exert a strong influence over successional pathways. Changes in water level and water chemistry that result from peat buildup and biological activity impart a strong directional aspect to further vegetation development. In this respect, the autogenic model of vegetation development does apply to both continental and oceanic peatlands. However, available data clearly indicate that allogenic factors can exert a strong influence on hydroseral pathways (Dachnowski 1926; Buell *et al.* 1968; Jackson *et al.* 1988; Yu *et al.* 1996). Walker (1970) concluded that variety is the key to hydroseral sequences, although he observed a strong tendency for development towards bog once *Sphagnum* had become established in a site. Given dramatic hydrological change, however, even a bog can revert to rich fen, as demonstrated by Glaser *et al.* (1990 1996) in Minnesota. Stratigraphic sequences indicate that wetlands can be stable for long periods of time (Holdgate 1955; Yu *et al.* 1996), and long-term ecological studies have demonstrated rapid vegetation change, usually in response to changes in hydrology or management (e.g. Jewell and Brown 1929; Spence 1964; Fojt and Harding 1995; van Diggelen *et al.* 1996; Gunnarsson *et al.* 2000).

Peatland development takes place within an environmental context that affects both rates of succession and probabilities of community transition, with development from fen to bog in particular being strongly dependent on climate. Autogenic succession is only one of several factors that influence peatland development, and its relative importance is likely to be dependent on climate. Based on the evidence reviewed above, I conclude the following:

1) Continental and oceanic peatlands are likely to differ in both the rate at which hydroseral sequences progress, and in the likelihood of individual community transitions.

2) Particularly during the later stages of hydroseral succession, allogenic factors are probably more important in continental than in oceanic sites.

3) Given the evidence available, it is questionable whether all continental peatlands have the potential to become ombrotrophic as a result of purely autogenic vegetation development.

THE CLYMO MODEL

Background

During recent decades, the main focus of peatland research has shifted towards carbon cycling, specifically the role of peatlands as sources or sinks of greenhouse gases such as carbon dioxide and methane. Predicting the impact of climate change on peatland carbon dynamics will require a mechanistic understanding of factors that control peat accumulation. Current views of long-term peat accumulation are largely based on a model proposed by Clymo (1984a). The Clymo model is attractive because of its conceptual simplicity, and it has been used extensively to infer decay parameters from ^{14}C- and ^{210}Pb- dated peat profiles (Warner *et al.* 1993; Charman *et al.* 1994; Belyea and Warner 1996; Clymo *et al.* 1998). However, the model makes several assumptions that potentially limit its applicability. Clymo himself stressed some of these limitations, and emphasized that the model was developed to describe the development of oceanic raised bogs, not peatlands in general (Clymo 1984a). In spite of this, patterns predicted by the model seem to be supported by a large body of evidence from different peatland types (Clymo *et al.* 1998).

The model

The Clymo model describes peat accumulation in terms of the balance between productivity and decay. It subdivides the peat profile into two layers (**acrotelm** and **catotelm** *sensu* Ingram 1978; Figure 1.2) that differ in the rate at which biological reactions take place. The upper acrotelm is aerobic for at least part of the year, whereas conditions in the catotelm are predominantly anaerobic. Because peatland water tables fluctuate on a periodic basis, the boundary between the two zones is gradual. Following Ivanov (1981), Clymo (1984a) identifies it with the minimum water table

depth in summer, averaged over several years. Organic matter enters the acrotelm at a rate p_a that is a function of productivity at the peatland surface. Because of incomplete decomposition, some of the organic matter in the acrotelm is eventually transferred to the catotelm. The annual rate of transfer is referred to as catotelm 'productivity', p_c.

Organic matter can be lost through decay in both the acrotelm and the catotelm. In its original form, the Clymo model assumes that decay is exponential, with mass loss per time interval a constant proportion of the amount of material present at the beginning of that time interval, i.e.

$$\frac{dm}{dt} = -\alpha m$$

where m represents organic matter mass, and α (T^{-1}) is the decay parameter or **decay coefficient**. Thus, mass remaining at any point in time can be calculated as:

$$m = m_0 e^{-\alpha t}$$

where m_0 is original mass and t is time. In its simplest form, the Clymo model uses two decay coefficients: one for the acrotelm (α_a) and one for the catotelm (α_c). It further assumes that acrotelm depth (mass), as well as productivity and decay parameters (p_a, p_c, α_a and α_c), are constant. Under this assumption, changes in mass loss per time interval depend only on catotelm mass, which gradually increases as peat accumulates.

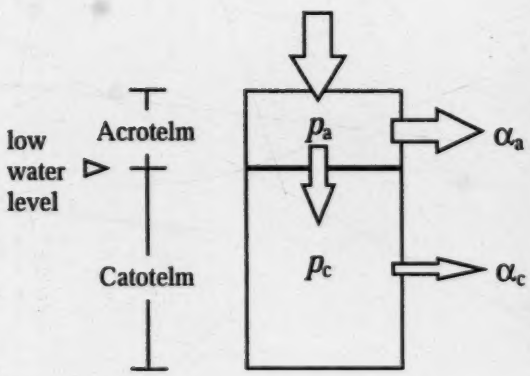


Figure 1.2: Structure and important parameters of the Clymo model. Net peat accumulation depends on the balance between productivity and decay in the aerobic acrotelm and anaerobic catotelm. p_a: Rate of organic matter addition to the acrotelm; α_a: Acrotelm decay constant; p_c: Rate of organic matter transfer from acrotelm to catotelm; α_c: Catotelm decay constant. Adapted from Belyea and Warner (1996)

The main point of Clymo's (1984a) paper is that, as long as total mass loss is a function of the organic matter mass present, peat will not accumulate indefinitely. Mass loss increases as the catotelm thickens, and the deposit will eventually reach a point at which total mass loss (from the entire profile) equals organic matter input at the surface. If this is the case, the Clymo model has several important implications: (1) the net ability of a peatland to sequester carbon decreases over time; (2) productivity at the surface bears no direct relation to net carbon sequestration, i.e. a peat deposit can have a neutral or even negative carbon balance even if peat actively accumulates at the surface; (3) plots of age or cumulative mass versus depth should show a concave pattern (Figure 1.3), and (4) long-term peat accumulation rates estimated from single (basal) ^{14}C dates depend partially on the age of the reference date, with older dates yielding lower (slower) rates (Figure 1.4). Hence, long-term (apparent) rates of peat accumulation should be compared with caution if they were calculated over different time spans (Tolonen *et al.* 1992, Clymo *et al.* 1998).

Evidence and applicability

Clymo repeatedly examined the evidence supporting or contradicting his model (Clymo 1984a; Clymo 1991; Clymo *et al.* 1998). Many peat profiles that meet model assumptions do show concave age / cumulative mass profiles. Exceptions include the most intensely dated peat profile available to date (Ikonen 1993), which shows a convex age / cumulative mass relationship supported by more than 120 ^{14}C dates. Rather than reviewing all available data, focus here will be on cases that do not conform to the predicted concave pattern, specifically in continental western Canada. Furthermore, the assumptions inherent in the Clymo model are stringent, and it seems worth considering (a) how representative sites that meet model assumptions are of peatlands in general (and of continental peatlands in particular), and (b) how useful the model is for projection of future peatland carbon dynamics, even if it adequately describes past accumulation patterns.

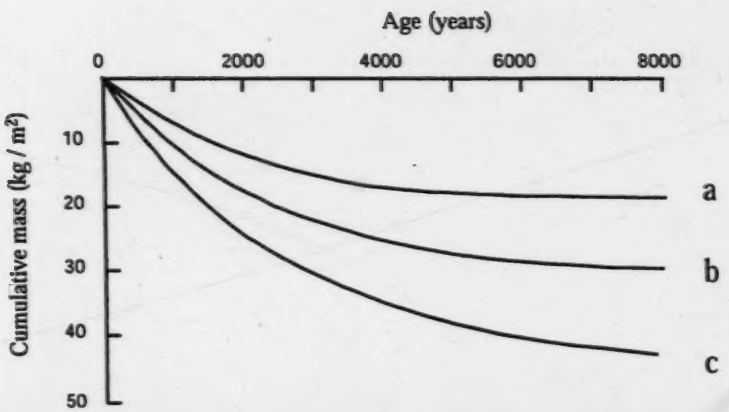


Figure 1.3: Hypothetical profiles of cumulative peat mass (above a given depth) and age of peat at that depth. Curves are concave because older core sections have lost a greater proportion of their original mass. Assuming equal productivity and acrotelm parameters, the three curves shown differ in α_c, with a > b > c.

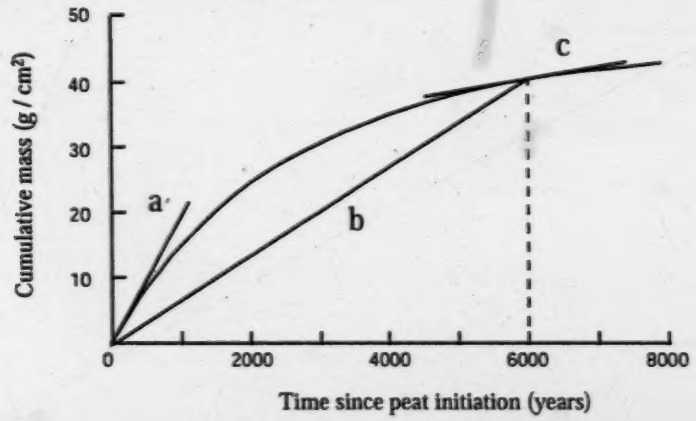


Figure 1.4: Different ways to report peat accumulation rates, and their relative magnitude according to the Clymo model. **(a) Original** rate (at time of initiation). Assuming constant productivity and decay, mass is added to the top of the peatland at this rate at any point in time. **(b) Long-term apparent** rate. Calculated by dividing total mass by basal peat age. This value is dependent on peatland age. **(c) Actual** rate. Reflects the balance between productivity and decay, i.e. describes net accumulation at any point in time. In order to estimate this rate, the Clymo model is fitted to a core profile with multiple dated levels, and parameters of the fitted model are used to calclate net mass accumulation. At any point in time after initiation, the relative magnitude of the three rates is a > b > c. Adapted from Clymo *et al.* (1998).

According to Clymo *et al.* (1998), the model can only be expected to describe peat accumulation if the following criteria are met: (1) the profile examined comes from close to the bog centre; (2) botanical composition is homogeneous, indicating that community composition (and thus, by inference, water table depth and water chemistry) have remained stable through time; (3) bulk density has been measured along the profile, and (4) at least eight ^{14}C dates are available. No cores from continental western Canada satisfy all four criteria. The most intensively dated profile available from the region is from a rich fen that has been dominated by *Scorpidium scorpioides* for most of its history. At this site, the relationship between cumulative mass and age is markedly convex (Yu 2002), i.e. shows a pattern opposite to that predicted by the Clymo model.

If the strict criteria listed above are relaxed, available data from continental western Canada show no clear pattern in the shape of cumulative mass / age profiles. Vitt *et al.* (2000) list nine cores with concave relationships (based on three ^{14}C dates each). Yu *et al.* (2000) review six examples of convex cumulative mass / age curves (based on 3-6 ^{14}C dates each). The latter include fens (Yu *et al.* 2000; Kubiw *et al.* 1989; Zoltai 1989) as well as bogs (Kuhry and Vitt 1996; Kuhry 1997). Both Kuhry and Vitt (1996) and Yu (2002) suggest that the observed convex pattern reflects either decreased productivity or an increase in acrotelm decomposition over time.

Relaxing model assumptions even further, Clymo *et al.* (1998) examined the relationship between cumulative carbon content and age in 795 Finnish peatlands, with each core represented by only one (basal) date. They used a slightly modified decay model in which proportional mass loss decreases linearly with the proportion of material remaining, reflecting increasing recalcitrance of organic matter. Cumulative mass / age profiles produced under this assumption do not approach an asymptotic value (i.e. peat can accumulate indefinitely, albeit at ever-decreasing rates). Fitting this model to the Finnish dataset showed a 'concave' pattern for bogs and a nearly straight relationship for fens. Clymo *et al.* (1998) attribute this difference to the more northerly distribution of fens rather than peatland type, and to a stronger effect of decreased

temperature on decay rates than on productivity. Permafrost peatlands for which multiple ^{14}C dates are available (Vardy *et al.* 1997; 2000) often show a 'convex' depth or cumulative mass / age relationship, most likely reflecting decreased accumulation following permafrost development. However, given the marked environmental changes associated with permafrost initiation, the applicability of the Clymo model is questionable in this situation.

The Clymo model has often been applied in situations that do not meet one or several of its basic assumptions, and it is hardly surprising that its predictions are not borne out in all cases. Most frequently violated is probably the assumption of constant mass input into the catotelm. As discussed in the first part of this chapter, community composition, water table depth, and chemical parameters tend to undergo marked, autogenically induced changes during peatland development. Although bogs and fens may not differ significantly in aboveground productivity (Thormann and Bayley 1997; Campbell *et al.* 2000), total productivity, acrotelm depth and decay parameters vary along the rich fen - bog gradient, reflecting both abiotic differences and chemical properties of the dominant vegetation (Bartsch and Moore 1985; Verhoeven and Toth 1995; Szumigalski and Bayley 1996). Thus, although the catotelm is the true site of peat accumulation, the rate at which it receives organic matter input is a function of acrotelm processes (Clymo 1984a; 1991), and these differ along the classic hydroseral sequence of peatland communities.

In spite of the fact that few situations are likely to meet all its assumptions, the Clymo model seems to work well in the type of system for which it was designed (i.e. coastal raised bogs). Fens, even if they undergo little community change, often do not seem to conform to model predictions. Clymo (1984a) expected peat accumulation dynamics in fens to be more complicated than in bogs, although he believed many of the processes involved to be similar in the two environments. Because of their continued dependence on groundwater input, fens cannot accumulate significant amounts of peat without either major community change or a gradual rise in the mineral water table (Kulczynski 1949). Fen water tables and peat accumulation

patterns are therefore likely to remain under stronger physiographic control than those of bogs.

Irrespective of its ability to explain long-term peat accumulation patterns, the Clymo model is unlikely to be of direct use in predicting responses of peatland carbon dynamics to climate change. Because it is concerned with long-term processes, the Clymo model represents acrotelm dynamics in a very simplistic manner. The acrotelm, however, will be most directly affected by climatic change, and predicting short-term changes in carbon sequestration will likely require more complex acrotelm-based models (Wieder 2001). In order to have any predictive power, such models should further be able to account for dynamic changes in both allogenic forcing mechanisms and peatland response, i.e., they should allow for changes in parameter values over time.

The Clymo model - Conclusions and further developments

In spite of the apparent criticisms raised above, the Clymo model remains a useful tool in understanding long-term peat accumulation dynamics. Using simple assumptions about decay, it illustrates that peat accumulation *in the absence of environmental change* does not continue indefinitely at its initial rate. Consequent implications for comparing long-term apparent accumulation rates or inferring net carbon sequestration from surface dynamics (Tolonen *et al.* 1993; Warner *et al.* 1993) have to be addressed by studies that examine peatland carbon dynamics. Further, because it is based on few parameters, the Clymo model allows for regional comparisons of long-term accumulation patterns (Tolonen *et al.* 1993; Korhola *et al.* 1995; Tolonen and Turunen 1996; Clymo *et al.* 1998.) It is questionable, however, whether the model itself can explain observed differences.

Peat profiles that fail to show the basic convex pattern predicted by the Clymo model imply that one or several of its basic assumptions have not been met. This is probably the case for most peatlands, particularly in continental regions where allogenic factors continue to exert strong control over development (see above). However, the way in which a model 'fails' is often instructive and allows for the

formulation of new hypotheses that can be examined using paleoecological data or further modelling (Yu *et al.* 2000; 2002).

Several recent studies have combined the basic ideas of the Clymo model with more dynamic conceptions of either hydrology or decomposition. Hilbert *et al.* (2000) adopted the same two-layer approach but incorporated several feedbacks between peat accumulation, water table dynamics and productivity. Frolking *et al.* (2001) developed a model that follows the fate of annual peat cohorts and allows for gradual changes in decay parameters with depth. Although they parameterized it for two peatland types (fen and bog), their model remains static in the sense that NPP and water table depth are assumed to be constant in time. Thus, stratigraphic changes cannot be generated by the model itself and have to be simulated by creating and superimposing separate fen and bog profiles. Wieder (2001) developed an empirical, cohort-style model by fitting NPP and depth-dependent decay parameters to ^{210}Pb dated acrotelm profiles. He then examined the impact of altered NPP and decay parameters on carbon sequestration over a 100-year timespan.

The three models described above incorporate more complex aspects of peatland dynamics than the original Clymo model. However, none of them accounts for basic ecological properties of peat-accumulating systems that should be taken into account in predictive models. Peatland vegetation responds dynamically to environmental change, be it autogenically and allogenically induced. Vegetation, in turn, affects peat accumulation through differential decay properties (Johnson and Damman 1993; Szumigalski and Bayley 1996). Thus, feedback processes between vegetation, hydrology and decay parameters are likely to have a strong impact on peat accumulation.

STRUCTURE OF THIS THESIS

The work that makes up this thesis is divided into three main chapters:

Chapter Two describes a case study that examines the development of a large peatland complex just north of Athabasca in the Continental Mid Boreal wetland

region (National Wetlands Working Group 1988) of central Alberta. The site is located close to the current southern limit of peatland distribution (Halsey *et al.* 1998). Long-term apparent accumulation rates, lateral peat expansion, and local vegetation succession are examined using sixteen core profiles, and results are discussed in the context of autogenic vegetation development, physiography, and the paleoclimatic history of the region.

Chapter Three, a second case study, uses a similar approach to examine the history of a peatland complex in the Rainbow Lake area of northwestern Alberta. The area is part of the Continental High Boreal wetland region (National Wetlands Working Group 1988) and the site is affected by discontinuous permafrost.

Chapter Four describes a simulation model that examines effects of community composition on peat accumulation over different timescales. It examines potential effects of litter-quality related variables on organic matter accumulation in different peatland types and critically examines our ability to infer past changes in organic matter dynamics from core profiles.

Chapter 5 is an overall discussion that examines implications of the results in the context of autogenic vegetation development and the Clymo model.

LITERATURE CITED

Aario L. 1932. Pflanzentopographische und paläogeographische Mooruntersuchungen in N-Satakunta. *Fennia* 55:1-179.

Aiton W. 1811. *A treatise on the origin, qualities and cultivation of moss-earth, with directions for converting it into manure*. Air. Glasgow.

Almquist-Jacobson H and Foster DR. 1995. Toward an integrated model for raised-bog development: Theory and field evidence. *Ecology* 76:2503-2516.

Auer V. 1921. Piirteitä Keski-Pohjanmaan soistumistavoista (Referat: Über Versumpfungsprozesse in Mittel-Österbotten). *Communicationes ex Instituto Quaestionum Forestalium Finlandiae* 3:1-71.

Bakker SA, van den Berg NJ and Speleers BP. 1994. Vegetation transitions of floating wetlands in a complex of turbaries between 1937 and 1989 as determined from aerial photographs with GIS. *Vegetatio* 114:161-167.

Bartsch I and Moore TR. 1985. A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Québec. *Canadian Journal of Botany* 63:1241-1248.

Begon M, Harper JL. and Townsend CR. 1990. *Ecology: Individuals, Populations and Communities*. 2nd Edition. Blackwell Scientific Publications. Oxford.

Belyea LR. 1996. Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland *Oikos* 77:529-539.

Belyea LR and Warner BG. 1996. Temporal scale and the accumulation of peat in a *Sphagnum* bog. *Canadian Journal of Botany* 74:366-377.

Bhiry N. 1996. Holocene plant succession in a dune-swale environment of southern Québec: A macrofossil analysis. *Ecoscience* 3:330-342.

Bridgham SD, Pastor J, Janssens JA, Capin C and Malterer TJ. 1996. Multiple limiting gradients in peatlands: A call for a new paradigm. *Wetlands* 16:45-65.

Buell MF, Buell HF and Reiners WA. 1968. Radial mat growth on Cedar Creek Bog, Minnesota. *Ecology* 49:1198-1199.

Bunting MJ and Warner BG. 1998. Hydroseral development in southern Ontario: patterns and controls. *Journal of Biogeography* 25:3-18.

Cajander AK. 1913. Studien über die Moore Finnlands. *Acta Forestalia Fennica* 2:298pp.

Campbell C, Vitt DH, Halsey LA, Campbell IK, Thormann MN and Bayley SE. 2000. *Net primary production and standing biomass in northern continental wetlands*. Information Report NOR-X-369. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta.

Carignan R and Kalf J. 1980. Phosphorus sources for aquatic weeds: water or sediments? *Science* 207:987-989.

Charman DJ, Aravena R and Warner BG. 1994. Carbon dynamics in a forested peatland in north-eastern Ontario, Canada. *Journal of Ecology* 82:55-62.

Clements, Frederic E. 1916. *Plant Succession: An analysis of the development of vegetation.* The Carnegie Institution of Washington. Washington.

Clymo RS. 1964. The origin of acidity in *Sphagnum* bogs. *The Bryologist* 67:427-431.

Clymo RS. 1984a. The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London* B 303:605-654.

Clymo RS. 1984b. *Sphagnum*-dominated peat: a naturally acid ecosystem. *Philosophical Transactions of the Royal Society of London* B 305:487-499.

Clymo RS, Turunen J and Tolonen K. 1998. Carbon accumulation in peatland. *Oikos* 81:368-388.

Clymo RS. 1991. Peat Growth. Pages 76-112 in: Shane LCK and Cushing EJ. (editors) *Quaternary Landscapes*. University of Minnesota Press. Minneapolis.

Conway VM. 1949. The bogs of central Minnesota. *Ecological Monographs* 19:173-206.

Dachnowski A. 1912. Peat deposits of Ohio. Their origin, formation and uses. *Geological Survey of Ohio, Fourth Series, Bulletin* 16:1-424.

Dachnowski AP. 1926. Profiles of peat deposits in New England. *Ecology* 7:120-135.

Devito KJ, Waddington JM and Branfireun BA. 1997. Flow reversals in peatlands influenced by local groundwater systems. *Hydrological Processes* 11:103-110.

Drexler JZ, Bedford BL, Scognamiglio R and Siegel DI. 1999. Fine-scale characteristics of groundwater flow in a peatland. *Hydrological Processes* 13:1341-1359.

du Rietz GE. 1949. Huvudenheter och huvudgränser i svensk myrvegetation (Main units and main limits in Swedish mire vegetation). *Svensk botanisk Tidskrift* 43:247-309.

du Rietz GE. 1954. Die Mineralbodenwasserzeigergrenze als Grundlage einer natürlichen Zweigliederung der Nord- und Mitteleuropäischen Moore. *Vegetatio* 5-6:571-585.

Eurola S. 1962. Über die regionale Einteilung der südfinnischen Moore (Suomalaisen Eläin-ja Kasvitieteellisen Seuran Vanamon Kasvitieteelisiä Julkaisuja). *Annales Botanici Societatis Zoologicae Botanicae Fennicae 'Vanamo'* 33:1-243.

Filion L and Bégin Y. 1998. Recent paludification of kettle holes on the central islands

of Lake Bienville, northern Québec, Canada. *The Holocene* 8:91-96.

Fojt W and Harding M. 1995. Thirty years of change in the vegetation communities of three valley mires in Suffolk, England. *Journal of Applied Ecology* 32:561-577.

Foster DR. 1984. The dynamics of *Sphagnum* in forest and peatland communities in southeastern Labrador, Canada. *Arctic* 37:133-140.

Frolking S, Roulet NT, Moore TR, Richard PJH, Lavoie M and Muller SD. 2001. Modeling northern peatland decomposition and peat accumulation. *Ecosystems* 4:479-498

Futyma RP and Miller NG. 1986. Stratigraphy and genesis of the Lake Sixteen peatland, northern Michigan. *Canadian Journal of Botany* 64:3008-3019.

Ganong WF. 1897. Upon raised peat-bogs in the province of New Brunswick *Proceedings and Transactions of the Royal Society of Canada* Series 2 Volume 3:131-163.

Geikie J. 1865. On the buried forests and peat mosses of Scotland and the changes of climate which they indicate. *Transactions of the Royal Society of Edinburgh* 24:363-384.

Glaser PH. 1987. The development of streamlined bog islands in the continental interior of North America. *Arctic and Alpine Research* 19:402-413.

Glaser PH, Bennett PC, Siegel DI and Romanowicz EA. 1996. Palaeo-reversals in groundwater flow and peatland development at Lost River, Minnesota, USA. *The Holocene* 6:413-421.

Glaser PH and Janssens JA. 1986. Raised bogs in eastern North America: transitions in landforms and gross stratigraphy. *Canadian Journal of Botany* 64:395-415.

Glaser PH, Janssens JA and Siegel DI. 1990. The response of vegetation to chemical

and hydrological gradients in the Lost River Peatland, Minnesota. *Journal of Ecology* 78:1021-1048.

Glaser PH, Siegel DI, Romanowicz EA and Shen YP. 1997. Regional linkages between raised bogs and the climate, grounwater, and landscape of north-western Minnesota. *Journal of Ecology* 85:3-16.

Godwin H and Bharucha FR. 1932. Studies in the Ecology of Wicken Fen II. The fen water table and its control of plant communities. *Journal of Ecology* 20:157-191.

Godwin H and Turner JS. 1933. Soil acidity in relation to vegetational succession in Calthorpe Broad, Norfolk. *Journal of Ecology* 21:235-262.

Gore AJP. 1983. Introduction. Pages 1-34 in: Gore AJP. (editor). *Mires: swamp, bog, fen and moor: General studies* . Ecosystems of the World 4A. Elsevier Scientific Publishing Company. Amsterdam.

Gorham E. 1953. Some early ideas concerning the nature, origin and development of peat lands. *Journal of Ecology* 41:257-274.

Gorham E. 1991. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* 1:182-195.

Granlund E. 1932. De svenska högmossarnas geologi. *Sveriges Geologiska Undersökning* C 373:1-193.

Green BH and Pearson MC. 1977. The Ecology of Wybunbury Moss, Cheshire. II. Post-glacial history and the formation of the Cheshire mere and mire landscape. *Journal of Ecology* 65:793-814.

Gunnarsson U, Rydin H and Sjörs H. 2000. Diversity and pH changes after 50 years on the boreal mire Skattlösbergs Stormosse, Central Sweden. *Journal of Vegetation Science* 11:277-286.

Halsey LA, Vitt DH and Bauer IE. 1998. Peatland initiation during the Holocene in Continental Western Canada. *Climatic Change* 40:315-342.

Halsey L, Vitt D and Zoltai S. 1997. Climatic and physiographic controls on wetland type and distribution in Manitoba, Canada. *Wetlands* 17:243-262.

Hansen K. 1959. The terms Gyttja and Dy. *Hydrobiologia* 13:309-315.

Heilman PE. 1966. Change in distribution and availability of nitrogen with forest succession on north slopes in interior Alaska. *Ecology* 47:825-831.

Heilman PE. 1968. Relationship of availability of phosphorus and cations to forest succession and bog formation in interior Alaska. *Ecology* 49:331-336.

Heinselman ML. 1970. Landscape evolution, peatland types and the environment in the Lake Agassiz Peatlands Natural Area, Minnesota. *Ecological Monographs* 40:235-261.

Heinselman ML. 1963. Forest sites, bog processes, and peatland types in the Glacial Lake Agassiz region, Minnesota. *Ecological Monographs* 33:327-374.

Hemond HF. 1980. Biogeochemistry of Thoreau's Bog, Concord, Massachusetts. *Ecological Monographs* 50:507-526.

Hilbert DW, Roulet N and Moore T. 2000. Modelling and analysis of peatlands as dynamical systems. *Journal of Ecology* 88:230-242.

Holdgate MW. 1955. The vegetation of some British upland fens. *Journal of Ecology* 43:389-403.

Huikari O. 1956. Primmäärisen soistumisen osuudesta Suomen soiden synnyssä (Untersuchungen über den Anteil der primären Versumpfung an der Entstehung der Finnischen Moore). *Communicationes Instituti Forestalis Fenniae* 46:1-79.

Ikonen L. 1993. Holocene development and peat growth of the raised bog Pesänsuo in southwestern Finland. *Geological Survey of Finland Bulletin*. 370:1-58.

Ingram HAP. 1978. Soil layers in mires: function and terminology. *Journal of Soil Science* 29:224-227.

Ivanov, KE. 1981. *Water Movement in Mirelands.* Acadamic Press. London.

Jackson ST, Futyma RP and Wilcox DA. 1988. A paleoecological test of a classical hydrosere in the Lake Michigan dunes. *Ecology* 69:928-936.

Jewell ME and Brown HW. 1929. Studies on northern Michigan bog lakes. *Ecology* 10:427-475.

Johnson L and Damman AWH. 1993. Decay and its regulation in *Sphagnum* peatlands. *Advances in Bryology* 5:249-296.

King W. 1685. Of the bogs, and loughs of Ireland. *Philosophical Transactions of the Royal Society* 15:948-960.

Klinger LF. 1990. Global patterns in community succession: 1. Bryophytes and forest decline. *Memoirs of the Torrey Botanical Club* 24:1-50.

Klinger LF. 1996a. Coupling of soil and vegetation in peatland succession. *Arctic and Alpine Research* 28:380-387.

Klinger LF. 1996b. The myth of the classic hydrosere model of bog succession. *Arctic and Alpine Research* 28:1-9.

Korhola A. 1992. Mire induction, ecosystem dynamics and lateral extension on raised bogs in the southern coastal area of Finland. *Fennia* 170:25-94.

Korhola A. 1995. Holocene climatic variations in southern Finland reconstructed from peat-initiation data. *The Holocene* 5:43-58.

Korhola A, Tolonen K, Turunen J and Jungner H. 1995. Estimating long-term carbon accumulation rates in boreal peatlands by radiocarbon dating. *Radiocarbon* 37:575-584.

Korpela L and Rainikainen A. 1996. Patterns of diversity in boreal mire margin vegetation. *Suo* 47:17-28.

Kratz TK and deWitt CB. 1986. Internal factors controlling peatland-lake ecosystem development. *Ecology* 67:100-107.

Kubiw H, Hickman M and Vitt DH. 1989. The developmental history of peatlands at Muskiki and Marguerite lakes, Alberta (Canada). *Canadian Journal of Botany* 67:3534-3544.

Kuhry P. 1997. The palaeoecology of a treed bog in western boreal Canada: a study based on microfossils, macrofossils and physio-chemical properties. *Review of Palaeobotany and Palynology* 96:183-224.

Kuhry P, Nicholson BJ, Gignac LD, Vitt DH and Bayley SE. 1993. Development of *Sphagnum* dominated peatlands in boreal continental Canada. *Canadian Journal of Botany* 71:10-22.

Kuhry P and Vitt DH. 1996. Fossil carbon / nitrogen ratios as a measure of peat decomposition. *Ecology* 77:271-275.

Kujala V. 1924. Keski-Pohjanmaan soiden synnystä (Ein Beitrag zur Kenntnis der Entstehung der Moore in Mittelösterbotten). *Communicationes ex Instituto Quaestionum Forestalium Finlandiae* 8:1-24.

Kulczynski MSt. 1949. Torfowiska Polesia: Peat bogs of Polesie. *Mémoires de l'Académie Polonaise des Sciences et des Lettres. Classe des Sciences Mathématiques et Naturelles Serie B: Sciences Naturelles* 15:1-356.

Kurz H. 1928. Influence of *Sphagnum* and other mosses on bog reaction. *Ecology*

9:56-69.

Lukkala OJ. 1933. Tapahtuuko nykyisin metsämaan soistumista (Vollzieht sich gegenwärtig Versumpfung von Waldboden). *Communicationes ex Instituto Quaestionum Forestalium Finlandiae* 19:1-127.

Mallik AU. 1995. Conversion of temperate forests into heaths: role of ecosystem disturbance and ericaceous plants. *Environmental Management* 19:675-684.

Malmström C. 1932. Om faran för skogsmarkens försumpning i Norrland (Über die Gefahr der Versumpfung des Waldbodens in Norrland (Nordschweden)). *Meddelanden från Statens Skogsförsöksanstalt* 26:1-162.

McIntyre SH, Duthie HC and Warner BC. 1991. Postglacial development of a marl and peat complex on the Precambrian Shield of northwestern Ontario. *Journal of Paleolimnology* 6:141-155.

Miller NG and Futyma RP. 1987. Paleohydrological implications of Holocene peatland development in northern Michigan. *Quaternary Research* 27:297-311.

Moore PD. 1973. The influence of prehistoric cultures upon the initiation and spread of blanket bog in upland Wales. *Nature* 241:350-353.

Moore PD and Beckett PJ. 1971. Vegetation and development of Llyn, a Welsh mire. *Ecology* 231:363-365

Moore PD and Bellamy DJ. 1974. *Peatlands*. Springer Verlag. New York

National Wetlands Working Group. 1988. *Wetlands of Canada*. Sustainable Development Branch, Environment Canada, Ottawa, Ontario, and Polyscience Publications Inc., Montréal, Québec.

Neiland BJ. 1971. The forest-bog complex of southeast Alaska. *Vegetatio* 22:1-64.

Noble MG, Lawrence DB and Streveler GP. 1984. *Sphagnum* invasion beneath an evergreen forest canopy in southeastern Alaska. *The Bryologist* 87:119-127.

Payette S. 1988. Late-Holocene development of subarctic ombrotrophic peatlands: allogenic and autogenic succession. *Ecology* 69:516-531.

Pearsall WH. 1917. The aquatic and marsh vegetation of Esthwaite water (Part I). *Journal of Ecology* 5:180-202.

Pearsall WH. 1918. The aquatic and marsh vegetation of Esthwaite water (Part II). *Journal of Ecology* 6:53-74.

Pearsall WH. 1920. The aquatic vegetation of the English Lakes. *Journal of Ecology* 8:163-201.

Pearsall WH. 1921. The development of vegetation in the English Lakes, considered in relation to the general evolution of glacial lakes and rock basins. *Proceedings of the Royal Society of London Series B* 92:259-284.

Romanowicz EA, Siegel DI and Glaser PH. 1993. Hydraulic reversals and episodic methane emissions during drought cycles in mires. *Geology* 21:231-234.

Siegel DI and Glaser PH. 1987. Groundwater flow in a bog-fen complex, Lost River peatland, northern Minnesota. *Journal of Ecology* 75:743-754.

Sjörs H. 1950a. On the relation between vegetation and electrolytes in North Swedish mire waters. *Oikos* 2:241-258.

Sjörs H. 1950b. Regional studies in North Swedish mire vegetation. *Botaniska Notiser* 173-222.

Sjörs H. 1980. An arrangement of changes along gradients, with examples from successions in boreal peatlands. *Vegetatio* 43:1-4.

Solem T. 1989. Blanket mire formation at Haramsøy, Møre og Romsdal, Western Norway. *Boreas* 18:221-235.

Spence DHN. 1964. The macrophytic vegetation of freshwater lochs, swamps and associated fens. Pages 306-425 in: Burnett JH. *The Vegetation of Scotland*. Oliver & Boyd. Edinburgh.

Spence DHN. 1982. The zonation of plants in freshwater lakes. *Advances in Ecological Research* 12:37-125.

Steffen, H. 1931. *Vegetationskunde von Ostpreussen*. Gustav Fischer. Jena.

Succow M and Jeschke L. 1990. *Moore in der Landschaft*. 2nd Edition. Verlag Harri Deutsch. Thun, Germany.

Swan MA and Gill AM. 1970. The origins, spread, and consolidation of a floating bog in Harvard pond, Petersham, Massachusetts. *Ecology* 51:829-840.

Szumigalski AR and Bayley SE. 1996. Decomposition along a bog to rich fen gradient in central Alberta, Canada. *Canadian Journal of Botany* 74:537-581.

Tallis JH. 1973. The terrestrialization of lake basins in north Cheshire, with special reference to the development of a 'Schwingmoor' structure. *Journal of Ecology* 61:537-567.

Tallis JH. 1983. Changes in wetland communities. Pages 311-347 in: Gore AJP. (editor). *Mires: swamp, bog, fen and moor: General studies* . Ecosystems of the World 4A. Elsevier Scientific Publishing Company. Amsterdam

Tallis JH. 1991. Forest and Moorland in the South Pennine uplands in the mid-Flandrian period: III. The spread of moorland - local, regional and national. *Journal of Ecology* 79:409-415.

Tansley AG. 1939. *The British Islands and their Vegetation*. The University Press.

Cambridge.

Tarnocai C, Adams GD, Glooschenko V, Glooschenko WA, Grondin P, Hirvonen HE, Lynch-Stewart P, Mills GF, Oswald ET, Pollett FC, Rubec CDA, Wells ED and Zoltai SC. 1988. The Canadian Wetland Classification System. Pages 413-427 in: National Wetlands Working Group. *Wetlands of Canada*. Sustainable Development Branch, Environment Canada. Ottawa, Ontario and Polyscience Publications Inc., Montréal, Québec.

Thormann MN and Bayley SE. 1997. Aboveground net primary production along a bog-fen-marsh gradient in southern boreal Alberta, Canada. *Écoscience* 4:374-384.

Thunmark S. 1940. Orientierung über die Exkursionen des IX. Internationalen Limnologenkongresses im Anebodagebiet. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 9:59-68.

Tikkanen M and Korhola A. 1993. Divergent successions in two adjacent rocky basins in southern Finland; a physiographic and palaeoecological evaluation. *Annales Academiae Scientiarum Fennicae, Series A III. Geologica - Geographica* 157:1-26.

Tolonen K. 1967. Über die Entwicklung der Moore im finnischen Nordkarelien. *Annales Botanici Fennici* 4:219-416.

Tolonen K, Vasander H, Damman AWH and Clymo RS. 1992. Rate of apparent and true carbon accumulation in boreal peatlands. Pages319-333 in: *Proceedings of the 9th International Peat Congress*. Uppsala, Sweden. 1992.

Tolonen K and Turunen J. 1996. Accumulation rates of carbon in mires in Finland and implications for climate change. *The Holocene* 6:171-178.

Tolonen K, Vasander H, Damman AWH and Clymo RS. 1993. Preliminary estimate of long-term carbon accumulation and loss in 25 boreal peatlands. *Suo* 43:277-280.

Tolonen M. 1987. Primary and secondary forest successions reflected in a late

Holocene pollen sequence from an upland mire near the SW coast of Finland. *Annales Botanici Fennici* 24:97-109.

Ugolini FC and Mann DH. 1979. Biopedological origin of peatlands in South East Alaska. *Nature* 281:366-368

van Breemen N. 1995. How *Sphagnum* bogs down other plants. *Trends in Ecology and Evolution* 10:270-275.

van Diggelen R, Molenaar WJ and Kooijman AM. 1996. Vegetation succession in a floating mire in relation to management and hydrology. *Journal of Vegetation Science* 7:809-820.

van Wirdum G, den Held AJ and Schmitz M. 1992. Terrestrializing fen vegetation in former turbaries in the Netherlands. Pages 323-360 in: Verhoeven JTA. *Fens and bogs in the Netherlands: vegetation, history, nutrient dynamics and conservation.* Kluwer Academic Publishers. Dodrecht.

Vardy SR, Warner BG and Aravena R. 1997. Holocene climate effects on the development of a peatland on the Tuktoyaktuk Peninsula, Northwest Territories. *Quaternary Research* 47:90-104.

Vardy SR, Warner BG, Turunen J and Aravena R. 2000. Carbon accumulation in permafrost peatlands in the Northwest Territories and Nunavut, Canada. *The Holocene* 10:273-280.

Verhoeven JTA and Toth E. 1995. Decomposition of *Carex* and *Sphagnum* litter in fens: effect of litter quality and inhibition by living tissue homogenates. *Soil Biology and Biochemistry* 27:271-275.

Vitt DH, Halsey LA, Thormann MN and Martin T. 1996. *Peatland Inventory of Alberta.* Alberta Peat Task Force, Network of Centres of Excellence in Sustainable Forest Management Grant, University of Alberta, Edmonton, Alberta.

Vitt DH, Halsey LA, Bauer IE and Campbell C. 2000. Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. *Canadian Journal of Earth Sciences* 37:683-693.

Vitt DH and Slack NG. 1975. An analysis of the vegetation of *Sphagnum*-dominated kettle-hole bogs in relation to environmental gradients. *Canadian Journal of Botany* 53:332-359.

Waddington JM and Roulet NT. 1997. Groundwater flow and dissolved carbon movement in a boreal peatland. *Journal of Hydrology* 191:122-138.

Walker D. 1970. Direction and rate in some British post-glacial hydroseres. Pages 117-139 in: Walker D and West RG. (editors). *Studies in the Vegetational History of the British Isles*. Cambridge University Press. Cambridge, UK.

Warner BG, Clymo RS and Tolonen K. 1993. Implications of peat accumulation at Point Escuminac, New Brunswick. *Quaternary Research* 39:245-248.

Warner BG, Kubiw HJ and Hanf KI. 1989. An anthropogenic cause for quaking mire formation in southwestern Ontario. *Nature* 340:380-384.

Weber CA. 1908. Aufbau und Vegetation der Moore Norddeutschlands. *Englers Botanische Jahrbücher. Beiblatt*. 90:19-34.

Wells CE, Hodgkinson D and Huckerby E. 2000. Evidence for the possible role of beaver (*Castor fiber*) in the prehistoric ontogenesis of a mire in northwest England, UK. *The Holocene* 10:503-508.

Wetzel RG. 1983. *Limnology*, 2nd edition. Saunders College Publishing. Fort Worth.

Wheeler BD and Proctor MCF. 2000. Ecological gradients, subdivisions and terminology of north-west European mires. *Journal of Ecology* 88:187-203.

Wieder K. 2001. Past, present, and future peatland carbon balance: an empirical model

based on ^{210}Pb-dated cores. *Ecological Applications* 11:327-342.

Wilcox DA and Simonin HA. 1988. The stratigraphy and development of a floating peatland, Pinhook Bog, Indiana. *Wetlands* 8:75-91.

Wilde SA, Voigt GK and Pierce RS. 1954. The relationship of soils and forest growth in the Algoma district of Ontario, Canada. *Journal of Soil Science* 5:22-39.

Wilson LR. 1935. Lake development and plant succession in Vilas county, Wisconsin. Part I. The medium hard water lakes. *Ecological Monographs* 5:207-247.

Yu Z, McAndrews JH and Siddiqi D. 1996. Influences of Holocene climate and water levels on vegetation dynamics of a lakeside wetland. *Canadian Journal of Botany* 74:1602-1615.

Yu Z, Vitt DH, Campbell C and Campbell ID. 2000. Pattern and processes of peat accumulation in continental rich fens: hypothesis and preliminary results. Pages 208-215 in: Rochefort L and Daigle J-Y. *Sustaining Our Peatlands. Proceedings of the 11th International Peat Congress*. Québec City, Canada. August 6-12 2000. Canadian Society of Peat and Peatlands and the International Peat Society. Canada.

Yu ZC. 2002. Does the convex pattern matter in understanding peat carbon dynamics? Pages 53-56 in: Yu ZC, Bhatti JS and Apps MJ. (technical coordinators). *Long-Term Dynamics and Contemporary Carbon Budget of Northern Peatlands*. Proceedings of the International Workshop on Carbon Dynamics of Forested Peatlands: Knowledge Gaps, Uncertainty, and Modelling Approaches. 23-24 March 2001, Edmonton, Alberta. Information Report NOR-X-383. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta.

Zobel M. 1990. Soil oxygen conditions in paludifying boreal forest sites. *Suo* 41:83-89.

Zoltai SC. 1988. Wetland Environments and Classification. Pages 1-26 in: National

Wetlands Working Group. *Wetlands of Canada*. Sustainable Development Branch, Environment Canada. Ottawa, Ontario and Polyscience Publications Inc., Montréal, Québec.

Zoltai SC. 1989. Late Quaternary volcanic ash in the peatlands of central Alberta. *Canadian Journal of Earth Sciences* 26:207-214.

Zoltai SC and Johnson JD. 1985. Development of a treed bog island in a minerotrophic fen. *Canadian Journal of Botany* 63:1076-1085.

Zoltai SC, Taylor S, Jeglum JK, Mills GF and Johnson JD. 1988. Wetlands of Boreal Canada. Pages 97-154 in: *Wetlands of Canada*. Sustainable Development Branch, Environment Canada. Ottawa, Ontario and Polyscience Publications Inc., Montréal, Québec.

CHAPTER 2

Importance of climate and physiography in controlling succession and rates of peat accumulation in central Alberta

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

INTRODUCTION

Peatlands are wetland ecosystems that accumulate carbon because primary productivity exceeds decomposition. Dead organic material builds up as peat, resulting in a net transfer of carbon from the atmosphere to the soil carbon pool. Most of the global peatland area is found in the boreal and subarctic zones of the northern hemisphere, and peatlands of this region represent a carbon store estimated at 270 - 455 petagrams (1 Pg = 10^{15} g; Turunen *et al.* 2002; Gorham 1991). This represents up to one third of the global soil carbon pool. In the Canadian prairie provinces (Alberta, Saskatchewan and Manitoba), peatlands cover 21% (365 000 km^2) of the available land base and store an estimated 48 petagrams of carbon (Vitt *et al.* 2000).

Peatlands are generally classified into geogenous fens and ombrogenous (rain-fed) bogs. Fens can be further subdivided into poor, moderate-rich and extreme-rich types that differ markedly in terms of water chemistry and vegetation composition (Vitt 1994). Poor fens are characterized by acidic surface waters (pH 4.0 - 5.5) that are low in base cations, and both poor fens and bogs have a ground cover dominated by peat mosses (*Sphagnum* spp). The vegetation of extreme-rich fens is dominated by monocots and brown mosses (mostly Amblystegiaceae), with surface waters that are neutral to basic (pH 7 or higher) and rich in base cations and alkalinity.

The gradient from fen to bog represents a common successional sequence that is often preceded by a lake or marsh phase (e.g., Weber 1908; Kuhry *et al.* 1993). Both allogenic and autogenic controls affect peatland development, and their relative importance at different stages of succession has been the subject of much debate (e.g., Sjörs 1980; Tallis 1983; Payette 1988; Kuhry *et al.* 1993). Most existing studies, however, concentrate on vertical peat sequences and ignore spatial aspects of peatland development. Peat can initiate not only through the infilling of shallow water bodies (terrestrialization), but also by direct establishment of peat in areas formerly occupied

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

by upland vegetation (paludification). Paludification is quantitatively more important and probably responsible for most of the global peatland area (Sjörs 1983).

Peatland distribution is controlled by complex interrelationships between climate, topography, substrate characteristics and hydrology. Climatic control over the geographic distributions of different peatland types is well documented (e.g. Eurola 1962; Damman 1979; Glaser and Janssens 1986). However, irrespective of the ultimate landform development that can be supported within a region, most peatlands initiate as fens, and the overall geographic distribution of peatlands is limited by the climatic threshold for fen development. Fen initiation depends on stable water tables that sustain the ground layer required for peat accumulation (Zoltai and Vitt 1990). In continental western Canada, peatlands are confined to regions that have a thermal seasonal aridity index (TSAI; mean annual precipitation / mean April to October temperature) of > 43 (Halsey *et al.* 1998). The southern limit of peatland distribution occurs within the Aspen Parkland Ecoregion (Halsey *et al.* 1998), with marshes and shallow open water being the dominant wetland classes further south (Adams 1988).

Even in areas where climate is suitable, peatland development is moderated by topography and local soil attributes such as salinity, pH and texture (Vitt 1994; Halsey *et al.* 1998). Community composition at newly paludified sites depends on the amount of available water and on the nutrient status of the underlying soil. Water availability, in turn, depends on the type of hydrological change that triggers paludification and on substrate permeability (Aario 1932). Basal peats of paludified sites can be woody, *Carex*- or *Sphagnum*-dominated, or comprise a mixture of these basic types (e.g. Aario 1932; Tolonen 1967; Korhola 1992). Further successional development is influenced by autogenic peat buildup, climate, topography, substrate permeability, and hydrology. The combined effects of these factors control modern landform distributions. Fens occupy gentle slopes where water input includes mineral runoff, whereas ombrotrophication occurs primarily in raised, flat areas or along drainage divides

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

(Kulczynski 1949; Heinselman 1970; Foster and Glaser 1986). The onset of peat formation within a watershed can profoundly affect drainage patterns and further landscape development (Heinselman 1970; Foster and Fritz 1987; Klinger and Short 1996).

Quantitative study of paludification requires multi-dimensional reconstruction of peatland development, i.e. both extensive survey data and multiple basal peat dates from individual sites. Detailed investigations of this type have largely been confined to raised bogs in coastal regions of Scandinavia (Foster and Wright 1990; Korhola 1992; 1994; 1996; Korhola *et al.* 1995a; Almquist-Jacobson and Foster 1995; Mäkilä 1997). Gauhl (1991) used pollen chronologies to study the initiation and expansion of a raised bog in the Rhön mountains of Germany, and both palynological methods and ^{14}C dating have been used to document patterns of peat initiation at site or landscape levels. This includes work by Tallis (1991) on blanket peats in northern England and Wales, as well as studies from Scotland (Charman 1994), Sweden (Foster and Fritz 1987), and eastern North America (Janssens *et al.* 1992; Brugam and McCance Johnson 1997; Lavoie and Richard 2000). Many of these studies have found local topography to be the most significant factor controlling the direction and speed of lateral peat expansion.

The relative importance of climate in controlling paludification rates is not clear. Mäkilä (1997) and Gauhl (1991) found little or no correlation between the intensity of lateral expansion and regional climate. When examining several sites, however, Korhola (1995) recognized two phases of relatively intensive paludification in southern Finland that seem to coincide with moist periods inferred from Swedish lake level data. Almquist-Jacobson and Foster (1995) reached a similar conclusion when investigating patterns in the paludification history of Swedish fens. Other allogenic factors that have been linked to widespread regional paludification include

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

human forest clearance (Tallis and Switsur 1990; Tallis 1991), forest fires (Huikari 1956), and impeded soil drainage following podzolisation (Ugolini and Mann 1979).

To date, there are few detailed studies that document the development of continental peatlands. Studies from boreal western Canada that have examined multiple cores from the same site (Kubiw *et al.* 1989; Nicholson and Vitt 1990) lack rigorous reconstruction of peat depth distributions and were not explicitly designed to examine site expansion. This study examines the development of a large peatland complex in boreal Alberta. Specifically, its aims are to (1) document temporal patterns of peat initiation and site expansion; (2) examine the nature of early peat-forming communities and their successional development through time; (3) compare long-term (apparent) rates of peat accumulation between site regions, and (4) investigate the relative importance of climate and physiography in controlling local patterns of peatland development.

STUDY AREA

The study site (Figure 2.1) is a large peatland complex located about 40 km north of the town of Athabasca in central Alberta (55 °03'N 113 °15'W). The area is part of the Continental Mid-Boreal Wetland Region, characterized by plateau, flat and basin bogs, as well as patterned, horizontal and basin fens (Zoltai *et al.* 1988). Regional upland vegetation is typical of the mixedwood section of the boreal forest (Rowe 1972) and consists of a mixture of *Populus tremuloides, Populus balsamifera, Picea glauca, Betula papyrifera* and *Abies balsamea*, with *Pinus banksiana* on sandy soils.. The landscape surrounding the site constitutes a diverse mosaic of upland forest and different peat landforms, with up to 20% of the land surface covered by peat.

The climate of the region is continental with cold winters and short, warm summers (Zoltai *et al.* 1988). The closest permanent weather station (Calling Lake RS; 55 °15'N, 113 °11'W; 598 m above sea level) has a mean annual temperature of 0.8 °C,

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

with daily means of -17.9 ℃ in January, and 15.9 ℃ in July. Mean annual precipitation is 463 mm (Canadian Climate Program 1993) and mostly falls as rain between May and September. The TSAI value for the station, calculated from the 1961-1990 normals (Canadian Climate Program 1993), is 47. According to criteria used by Halsey *et al.* (1998), this suggests that regional climate is potentially limiting for peatland development.

Continental glaciers retreated from the region between 12000 and 11000 yr BP (*ca.* 14,000-13,000 cal. yr BP; Dyke and Prest 1987). Bedrock consists of Cretaceous grey and dark grey marine shales of the LaBiche Formation that are overlain by Quaternary deposits. Detailed soil survey data are not presently available for the area, but exploratory survey results (Wynnyk *et al.* 1964), and information available for the region immediately south of the study area (Kjearsgaard 1972), suggest that the site is underlain by till, most likely medium-textured clay loam till derived from the LaBiche Formation. Regional topography is level to undulating, with slopes of less than 1.5 percent (Wynnyk *et al.* 1964).

Given the complex mixture of upland and different peat landforms characteristic of the region and the consequent lack of clear site boundaries, a subregion of the peatland complex was selected for detailed investigation. This 9.5 km^2 study area (Figure 2.2) is largely bounded by upland, and its northern end occupies an elevation of about 670 m. It is located at the southern margin of a ridge that constitutes a local drainage divide between two tributaries of the Athabasca River. The area occupied by the site gently slopes southwards from this divide.

The most prominent landform within the study area is a large, partially open fen that occupies most of the southeastern part of the study area (Figure 2.2). Tree cover, where present, consists of stunted *Larix laricina*, with scattered *Betula glandulosa* and *Salix* spp. in the shrub layer (Figure 2.3a). The ground layer is made up of *Carex* spp. and a dense cover of bryophytes indicative of rich fen conditions,

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

such as *Sphagnum warnstorfii*, *Tomenthypnum nitens*, and *Hamatocaulis vernicosus*. The southern end of this fen is flanked by two small upland outcrops that seem to form a topographic constriction, possibly impeding southward drainage. The region north and north-west of the open fen is occupied by a mixture of peatland (mostly treed fen) and small upland outcrops. The canopy of the treed fen is made up by varying proportions of *Picea mariana* and *Larix laricina*. *Salix* sp. are found in swampy areas, and some individuals of *Pinus banksiana* grow on shallow peat, usually in close proximity to uplands. The understorey reflects this diversity, comprising taxa associated with poor fen, bog, or upland habitats. The northern end of the study site and some regions along its western edge (Figure 2.2), are occupied by bog, characterized by a canopy of stunted *Picea mariana* over *Ledum groenlandicum*, *Vaccinium vitis-idea*, *Rubus chamaemorus* and *Eriophorum vaginatum* (Figure 2.3b). Bryophyte cover is close to 100% and consists mostly of *Sphagnum fuscum*, with *S. magellanicum* and *S. angustifolium* in wetter areas.

METHODS

Field sampling

The site was surveyed in September 1996 and June 1998. A metal probe was used to measure peat depth at 25, 50 or 100 m intervals along a series of transects. Placement of transects was partially dictated by accessibility, but an attempt was made to distribute them evenly throughout the site. Survey points were discarded if seasonal frost prevented probing to the mineral substrate, yielding a total of 311 points with reliable depth measurements. Sixteen coring sites were selected from these points to encompass the range of peat depth and landform diversity present at the site. Peat cores were taken using a modified 5 cm diameter Macaulay peat sampler (Figure 2.4) and stored in half-sections of 1 m long PVC pipe wrapped in plastic film. Duplicate cores were taken at shallow sites (nos. 1, 2, 3, 5, 10 and 14 in Figure 2.2).

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Spatial analysis

Peat depth throughout the study area was interpolated from the depth measurements using geostatistical methods (e.g. Journel and Huijbregts 1978; Isaaks and Srivastava 1989). Because high (deep) values were concentrated in the eastern half of the site, five upland boundary points were added in the northern bog area and a cubic trend surface was fitted to the data by generalized least squares. The residual variogram was fitted with a spherical model. The variogram model (Figure 2.5) is markedly anisotropic, with greatest spatial continuity of depth values in a north / north-easterly direction (15 °). Depth distribution throughout the site was predicted on a 25 m × 25 m grid by non-stationary simple kriging using the cubic trend surface values as local means (program kt3d in GSLIB; Deutsch and Journel 1998). Jacknifing indicated that this procedure was less prone to bias and more robust to altered input data configurations than ordinary kriging without prior fitting of a trend surface.

Physico-chemical analysis and ^{14}C dating

Samples for physico-chemical analysis (2.5 - 5.0 cm^3) were taken at 10 cm intervals along all cores, air-dried for 48 hours, ground to a fine powder and combusted for four hours at 550 °C to measure organic matter content. A bulk peat sample (3 or 4 cm in length) was removed from the base of each core (or, if two cores were available, from the base of each replicate), dried at 80 °C for 24 hours and submitted to the radiocarbon laboratory of Brock University (BGS) for ^{14}C age determination. A second sample was taken from immediately above the ^{14}C sample, and a portion of it was retained for macrofossil analysis. All dates were calibrated in CALIB rev.4.1 (Stuiver and Reimer 1993) using the INTCAL98 dataset (Stuiver *et al.* 1998) and method B (probability distribution). Calibration curves were smoothed assuming that one cm of peat represents 20 years of accumulation. This number is close to the average long-term accumulation rate for the 16 cores.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

For the purpose of this study, 'basal peat' is defined as the deepest section of each core with an organic matter content of ≥ 80%. Published classification schemes for organic soils differ in the amount of mineral a material can contain and still be considered peat, with some systems allowing for as much as 50-55% mineral content (see Clymo 1983, Andrejko *et al.* 1983). The '20% ash limit' used here is based on a large dataset of peat samples from western Canada (Zoltai *et al.* 2000) that suggests that the only peat type with mineral contents consistently higher than 20% is limnic peat. Basal limnic deposits were deliberately excluded because lake infilling can occur under conditions that are too dry for paludification (Nicholson and Vitt 1994).

Long-term apparent rates of peat accumulation (*sensu* Clymo *et al.* 1998) were calculated for all cores from the depth and ^{14}C age of basal peat samples. Comparison of bulk density values calculated after air drying for 48 hours with values obtained by oven-drying adjacent samples at 75 ℃ for 36 hours showed that air-drying resulted in significantly higher bulk density values, especially in heavier samples. Since oven-dried values are not available for most of the cores, accumulation rates presented here do not incorporate bulk density and are therefore rates of *height* rather than mass accumulation. Based on the same set of samples, percent ash values calculated after air drying tend to be lower than those calculated after oven-drying, especially in samples of high bulk density. At the 20% ash cutoff used to delineate basal peat, the resulting error is about one percent, i.e., a calculated value of 20 percent ash corresponds to an actual value of 21 percent. Since ash content generally increased abruptly at the base of core profiles and ^{14}C dates were obtained from bulk samples, this error is considered negligible in terms of defining basal peat. However, loss-on-ignition data will not be plotted for individual cores.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Macrofossil analysis

Macrofossil samples (2.5 - 5 cm^3) were removed from all cores at 10 cm intervals, half-way between samples for physico-chemical analysis. Botanical composition was scored under a dissecting microscope using a modified version of the Troels-Smith system (Aaby and Berglund 1986). *Sphagnum*, other bryophytes, herbaceous, and woody remains were each assigned a score from zero to four, with scores for each sample summing to four. Materials that were present at frequencies too low to receive a score of one were recorded as traces. Later, a value of 0.25 was assigned to each trace and sample scores were re-standardized to sum to four. A three-point moving average of the resulting values was used to assign each sample to one of five broad peat types (Figure 2.6). Samples from cores 3, 10, 16, 17 and 18 (Figure 2.2) were further subjected to more detailed macrofossil analysis, as were basal samples from all 16 cores. A subsample was distributed evenly on a channeled plexiglass template, and percent frequencies were estimated for all bryophyte taxa and selected categories of vascular plant remains. Reference material used in macrofossil determination and concepts used for important macrofossil taxa are listed in Appendix 2. Nomenclature follows Moss (1983) for vascular plants, Anderson (1990) for *Sphagnum* and Anderson *et al.* (1990) for other mosses.

Statistical analysis of macrofossil data

Clustering and ordination

Macrofossil samples from cores 3, 10, 16, 17 and 18 (n = 136) were grouped into clusters using Ward's minimum variance method (Ward 1963). Species indicator values for the resulting cluster groups were calculated following the method of Dufrêne and Legendre (1997). In this method, the relative abundance of a taxon j in cluster k (RA_{jk}) and the relative frequency at which taxon j occurs in samples from cluster k (RF_{jk}) are combined into an indicator value (IV) of taxon j for cluster k:

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

$$IV_{kj} = RA_{kj} \times RF_{kj} \times 100$$

An IV of 100 denotes a perfect indicator, i.e. a species that occurs in all samples from cluster *k* and is absent from all other clusters. The significance of indicator values is tested by a Monte Carlo procedure. Macrofossil data were also subjected to ordination by detrended correspondence analysis (DCA; Hill and Gauch 1980). All analyses were run in PC-ORD (McCune and Mefford 1999).

Core zonation

Because of the small samples size and relatively coarse sampling resolution, macrofossil composition sometimes fluctuated erratically between stratigraphically adjacent samples. In order to reduce this variability, data from each of the five cores were converted to presence / absence values and subjected to stratigraphically constrained cluster analysis, again using Ward's minimum variance method (Ward 1963; Birks 1986). A variance cutoff of 5.0 (Squared Euclidean distance) was used to delineate stratigraphic zones. While somewhat arbitrary, this cutoff gave a reasonable number of zones and avoided, with one exception, interpretation problems associated with reversals (i.e. the joining of two adjacent clusters leading to a *decrease* in within-cluster dispersion).

Environmental interpretation of successional trends

Indicator values and tolerance ranges for pH, depth to water table, corrected conductivity (k_{corr}) and selected cation concentrations (Na, K, Ca and Mg) were calculated for each of the macrofossil taxa from a large dataset for western Canada (Gignac *et al.* 2000). All variables except pH were log transformed, and environmental indicator values and tolerance ranges for each taxon were calculated from the resulting distributions by weighted averaging (ter Braak and Barendregt 1986; Birks *et al.* 1990):

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

$$\hat{u}_j = \sum_{i=1}^{n} y_{ij} \times x_i \Big/ \sum_{i=1}^{n} y_{ij}$$

and

$$\hat{t}_j = \left[\sum_{i=1}^{n} y_{ij} \times \left(x_i - \hat{u}_j \right)^2 \Big/ \sum_{i=1}^{n} y_{ij} \right]^{\frac{1}{2}}$$

where $\hat{u}$ is the indicator value for taxon j and $\hat{t}$ its tolerance range or weighted standard deviation, y_{ij} is the abundance of taxon j in sample i, and x_i is the measured value for the environmental variable in sample i. In cases where macrofossil taxa could not be assigned to single species, indicator values were calculated for groups of species that most closely corresponded to the macrofosil categories. The indicator value and tolerance range for 'robust woody roots', for example, are based on combined data for non-ericaceous woody taxa (*Picea mariana, Larix laricina, Betula glandulosa / B. pumila* and *Salix* spp.); values for the category 'herbaceous' are based mainly on data for *Carex* and *Eriophorum* spp.

Values of environmental variables were estimated for each macrofossil sample by weighted averaging of macrofossil indicator values, with the weight assigned to each taxon inversely proportional to its environmental tolerance (ter Braak and Barendregt 1986; Birks *et al.* 1990):

$$\hat{x}_i = \sum_{j=1}^{m} \frac{y_{ij} \times \hat{u}_j}{\hat{t}^2{}_j} \Big/ \sum_{j=1}^{m} \frac{y_{ij}}{\hat{t}^2{}_j}$$

where $\hat{x}_i$ is the inferred value of the environmental variable for sample i. Inferred values were used to overlay environmental vectors on the ordination by multiple regression (Dargie 1984; ter Braak 1995).

RESULTS

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Peat depth interpolation

Peat depths > 400 cm occur in two separate basins in the eastern part of the study area: one underneath the northern bog and the second below the open fen area (Figure 2.7). Slopes leading into these basins are generally steep, especially along the western and eastern margins of the fen. The two basins are connected by a narrow channel with peat depths of 200-250 cm. In the western parts of the site, peat is mostly less than 150 cm thick, although depth exceeds 300 cm in several locations.

Core lithologies

The 16 cores differ markedly in stratigraphy, with all five of the basic peat types found in basal samples. Cores 7, 11, 16, 17 and 18 (group A) represent the deepest peat deposits at the site and are dominated by herbaceous / moss peat at the time of initiation (Figure 2.8a). Basal samples from cores 16 and 18 contain *Typha* seeds, and single *Chara* oogonia were found in cores 7, 16 and 18. Basal sediments (below ^{14}C depth) from these three cores contained marl ($CaCO_3$). Cores 16 and 18 are both presently *Sphagnum*-dominated. The three fen cores contain pure or woody herbaceous / moss peat throughout, except for core 7 which is capped by about 20 cm of *Sphagnum* peat overlying a water lens. Several of the open fen cores have a gap in their stratigraphy just below the surface, pointing towards either a water lens or a layer of very loose, watery peat that was lost during coring.

A second group of cores (group B; cores 2, 4, 8, 12, 13 and 15) represents areas of intermediate (150 - 250 cm) peat depth and is characterized by either woody or woody / herbaceous deposits at the time of peat initiation (Figure 2.8b). These sites are located on the sloping sides of the two large basins (cores 8, 12, 13 and 15) or in deep channels that connect to the open fen at its northern edge (cores 2 and 4). Basal peats of cores 2, 8 and 15 contain charcoal. With one exception (core 4), all cores in this group contain *Sphagnum* at the surface. In core 15 (northern bog basin), the *Sphagnum*

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

peat is 120 cm thick, whereas cores associated with the open fen basin (nos 2, 8, 12 and 13) are capped by a thin (20-30 cm) *Sphagnum* layer that overlies herbaceous deposits .

The five shallowest cores (group C; cores 1, 3, 5, 10 and 14) contain basal deposits of either pure or woody *Sphagnum* peat (Figure 2.8c). Loss-on-ignition data indicate that the *Sphagnum* peat overlies mineral material, and cores 5 and 10 contain charcoal at or close to the peat/mineral interface. In cores 3, 5 and 14, the basal *Sphagnum* peat is overlain by woody sedge peats, and cores 3 and 5 contain only traces of *Sphagnum* at the surface. Figure 2.9 summarizes the overall development of the 16 cores.

Macrofossil analysis

Macrofossil diagrams for cores 3, 10, 16, 17 and 18 are shown in Appendix 3. Zones plotted on these diagrams (and used in subsequent analyses) do not necessarily match the lithological zones plotted in Figure 2.8. This reflects sampling error (resulting from small sample sizes) as well as the different classification methods used. Zones calculated from the more detailed macrofossil information (Appendix 3) often reflect changes (such as changing dominance of different *Sphagnum* species) that are not detectable by the lithological classification.

Clustering and ordination

Clustering of macrofossil samples was terminated at the eight-cluster level. Final clusters and their indicator species are summarized in Table 2.1. *Sphagnum angustifolium*, *S. magellanicum* and *S. fuscum / S. capillifolium* (the latter not separated in macrofossil determination) each are associated with one cluster (nos 8, 4 and 3 respectively), all with high indicator values. Cluster 3 (*S. fuscum / S. capillifolium*) includes basal samples from cores 1, 3, 10 and 14. Cluster group 2 (wood and bark remains) includes basal samples from cores 4, 5, 8, 12, 13 and 15.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Robust woody roots, *S. warnstorfii* and *Aulacomnium palustre* are indicator taxa for cluster group 1, which contains the basal sample from core 2. Cluster 5 contains 34 samples including the basal sample from core 18. Indicator taxa are smooth woody roots and dicot leaves, and herbaceous remains reach a high relative abundance. *Calliergon giganteum* is a near-perfect indicator for cluster 6. Herbaceous remains are the only significant indicator taxon for cluster 7, which consists of samples that contain almost no other remains. Basal samples from the four deepest cores (no. 7, 11, 16 and 17; Figure 2.8a) are included in this last cluster. The coefficient of determination between distances on the ordination diagram (Figure 2.10) and in the original data matrix indicates that 69% of the variability in the macrofossil data is explained by the first two ordination axes (McCune and Mefford 1999). Most clusters separate well on the ordination diagram except for cluster 7, which is contained within cluster 5. Samples from cluster 1 overlap with those of clusters 2, 3 and 4.

Inferred environmental change through time

Mean indicator values and tolerance ranges for water table depth, pH and conductivity calculated for macrofossil taxa are shown in Figure 2.11. Taxa are tightly spaced along all three gradients, except for an apparent discontinuity in the indicator values for pH at about pH 5.5. Bryophytes generally have narrower tolerance ranges along the pH and water table gradients than vascular plant categories.Vectors showing inferred directions of maximum change in pH, depth to water table and K_{corr} are superimposed on the macrofossil ordination in Figure 2.12a. All vectors are scaled to the same (arbitrary) length. Depth to water table is associated with both ordination axes but varies most strongly along axis 1. Corrected conductivity, pH and cations examined are associated with axis 2, all increasing towards the top of the ordination diagram.

Sequences of vegetation succession in cores that were subjected to detailed macrofossil analysis are summarized in Figure 2.12b-e. Each numbered point

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

represents a vegetation zone, as defined by stratigraphically constrained clustering along cores. For each core, zones are numbered from the base upwards, and the mean and range of axis scores within each zone are indicated on the plot. Cores 3 and 10 (Figure 2.12b and c) are dominated by *Sphagnum fuscum* / *S. capillifolium* at the time of initiation (macrofossil cluster group 3 in Figure 2.10), and all samples from core 10 fall into one macrofossil zone. Samples from the upper zone of core 3 contain *Sphagnum warnstorfii* and *Aulacomnium palustre* (cluster 1 in Figure 2.10). Site 3 is located at the margin of the southern fen basin, and inferred environmental data indicate that local conditions became wetter in the course of its development.

The environment at coresite 17 (Figure 2.12e) seems to have changed little since the onset of peat formation. In this core, constrained clustering produced ambiguous results. When combined, the three zones plotted in Figure 2.12e fall below the variance cutoff used, suggesting that the entire core represents one vegetation zone.

Cores 16 and 18 (Figure 2.12d and f) both represent deep basins. Zone 1 of core 16 comprises 10 samples that mostly fall into macrofossil cluster groups 5 and 7 (smooth woody roots / dicot leaves; herbaceous remains). Zone 2 only contains two samples, and inferred environmental values indicate a rapid decrease in K_{corr} and pH between zones 1 and 3. Zones 3 to 6 are mostly *Sphagnum*-dominated (macrofossil cluster groups 3, 4 and 8), and seem to differ mainly in their relative depth to water table. Core 18 begins its development in the same region of the ordination diagram as core 16, and each successive vegetation zone indicates slightly lower pH and conductivity than that preceding it. There is no evidence for fluctuations in water level of the kind observed in core 16, but coresite 18 appears to be drier today (zone 5) than it was when peat accumulation first began.

Basal dates and rates of peat accumulation

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Radiocarbon dates for basal peat samples span almost 6000 calendar years (Table 2.2). The oldest date (7450 cal. yr BP) was measured in the northern bog basin (core 16), and peat initiation in the treed fen area occurred less than 500 years later (Core 18; 7020 cal. yr BP). The oldest date in the open fen (6020 cal. yr BP) comes from core 11 at the southern end of the study area. At the northern end of the fen basin, peat initiation is more recent, with basal dates for cores 1-5 mostly between 2000 and 3000 cal. yr BP. The youngest basal date was measured in the western bog area (core 10; 1560 cal. yr BP).

Overall, there is a significant positive correlation ($r = 0.78$; $p < 0.01$) between the age and depth of basal peat (Figure 2.13). Rates of peat accumulation range from 0.29 to 0.94 mm $year^{-1}$ (Table 2.2) and seem to differ systematically between regions: Cores 2, 4, 7, 11 and 17, all located in deep channels that underlie the open fen basin, show the fastest rates of peat accumulation. This is true even if gaps in their stratigraphy (Figure 2.8) are interpreted as water lenses and subtracted from the total core depth, although Core 16 (northern bog basin) then shows the same rate of peat accumulation as core 11. Slow accumulation rates (< 0.4 mm $year^{-1}$) were observed in cores 13, 14, 15 and 18. Long-term peat accumulation rates are positively correlated ($r = 0.53$, $p = 0.02$) with the amount of herbaceous material in the peat column (mean score for herbaceous material), and negatively correlated with the mean score for *Sphagnum* ($r = -0.58$, $p = 0.01$; Figure 14).

INTERPRETATION

Local community succession

Clustering of macrofossil data for cores 7, 10, 16, 17 and 18 identified a number of distinct community types. Cluster groups 8 (*S. angustifolium*), 4 (*S. magellanicum*) and 3 (*S. fuscum* / *S. capillifolium*) represent hollow, intermediate, and hummock habitats in poor fen or bog. Clusters 5 (smooth woody roots / dicot leaves),

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

6 (*Calliergon giganteum*) and 7 (herbaceous) come from fen environments. Cluster 7 includes marshes as well as open monocot fens, and cluster 5 is tentatively classified as shrubby monocot fen. Herbaceous remains are abundant in this cluster, and dicot leaves mostly belonged to *Betula* or *Salix* spp, both of which are abundant in fen areas today. *Calliergon giganteum* (cluster group 6) is a characteristic species of moist carpets in moderate-rich fens (Chee and Vitt 1989).

Group 1 (robust woody roots / *S. warnstorfii* / *A. palustre*) represents transitional moderate-rich fen communities. This is supported by the intermediate position of this group on this ordination diagram, and by ecological affinities of its component species. *Sphagnum warnstorfii* is a characteristic species of moderate-rich fens (Gignac *et al.* 1991), and *A. palustre* is a hummock species with wide ecological amplitude (Nicholson and Gignac 1995). Robust woody roots appeared to be mostly ectomycorrhizal, and are likely to represent a variety of taxa. Most common trees and non-ericaceous shrubs in western Canadian peatlands are known to form ectomycorrhizal associations (Thormann *et al.* 1999a), limiting the diagnostic utility of this character. Cluster 2 (wood and bark remains) contains most of the basal samples from cores in group B (Figure 2.8b). This cluster most likely represents newly paludified forest sites or woody peatland microenvironments.

Lithological data and more detailed macrofossil analysis both suggest that the five deepest cores initiated under wet conditions, most likely as open fens or marshes (Figures 2.8a; 12d, e and f). Shallow lakes may have been present initially, but loss-of-ignition curves do not suggest extensive limnic deposits at any of the sites. Cores of intermediate depth (Figure 2.8b) mostly initiated through conversion of upland forest to sedge fen, either directly or via a brief marsh phase resulting from local or seasonal flooding. Shallow cores (Figures 2.8c; 2.12b and c) initiated by invasion of *Sphagnum* into upland forest. There is a general trend towards *Sphagnum*-dominated peat types at the surface (Figure 2.9; 12b, c, d and f), as predicted by autogenic models of peatland

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

succession (Weber 1908). However, in several of the cores transition to *Sphagnum* seems recent, and Cores 3 and 5 show an apparently reverse sequence with *Sphagnum*-dominated peat at the base and surface deposits of moss / herbaceous peat. In four of the cores (no. 4, 11, 10 and 14) little net community change has occurred over time.

DISCUSSION

Peatland initiation and landscape succession

The Athabasca peatland is located about 350 km north of the transition from grassland to boreal forest, and about 100 km north of the boundary between the Aspen Grove and Mixedwood sections of the Boreal forest (Rowe 1972). The transition from southern boreal forest to Aspen Parkland and prairie is characterized by steep environmental gradients, with summer temperatures increasing and effective moisture decreasing southwards (Ritchie and Harrison 1993). Palynological evidence indicates that grasslands extended north of their present range over large parts of western Canada from ca. 10,000 to 7000 cal. yr BP (Ritchie 1976; Vance *et al.* 1995). Major climatic boundaries were displaced northwards during this period (Harrison and Metcalfe 1985; Ritchie and Harrison 1993), and conditions were warmer and drier than they are today (Ritchie 1976; Zoltai and Vitt 1990; Ritchie and Harrison 1993; Vance *et al.* 1995). Peat initiation at Athabasca occurred towards the end of this early Holocene warm period, and over the following millenia the peatland developed within a context of climatic cooling and associated regional vegetation change.

Before 7000 cal. yr BP

The flooding of shallow lake basins that were dry during the early Holocene started as early as 8200 cal. yr BP in Alberta and continued until about 3200 cal. yr BP (Schweger and Hickman 1989). Larger basins that had flooded in the early Holocene showed reduced water levels during the warm period. At Moore Lake (54°30'N

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

110 30'W; Figure 2.1), changes in diatom assemblages and the presence of *Ruppia occidentalis* suggest increased salinity. Schweger and Hickman (1989) and Hickman and Schweger (1996) infer a 15 m drop in water level between 10200 and 7000 cal. yr BP from the increased abundance of epipelic diatoms, and palynological evidence suggests that open grassland surrounded the lake 7000 years ago.

Lofty Lake (54 44'N, 112 29'W; Figure 2.1) was reduced in size between ca. 9600 and 7200 cal. yr BP (Vance *et al.* 1995), and its pollen record suggests a northward shift of the prairie / parkland boundary (Lichti-Federovich 1970; Vance *et al.* 1995). Parkland did not reach Mariana Lake (55 57'N, 112 01'W; Figure 2.1), but the pollen record from this site nevertheless shows changes in species composition that suggest increased aridity. *Typha* was abundant between about 8200 and 6300 cal. yr BP, indicating shallow or fluctuating water levels (Hutton *et al.* 1994). The Mariana Lake peatland initiated around 9100 cal. yr BP, but these early peat deposits were mostly the result of localized lake infilling (Nicholson and Vitt 1990).

Farther south at Athabasca, the northern bog area (core 16) and at least one basin in the present-day treed fen (core 18) started accumulating peat independently around 7000 cal. yr BP (Figure 2.15). Both cores contain mollusk remains at the base, suggesting that they initiated as shallow ponds or marshes. Initial peat-forming communities were monocot-dominated, and supersaturated conditions led to the precipitation of marl at coresite 16. The onset of climatic cooling most likely led to changes in the regional moisture balance that allowed for the development of shallow open-water areas in isolated topographic depressions. This promoted the onset of peat accumulation in localized situations.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

7000 - 5000 cal. yr BP

After 7000 cal. yr BP, climatic cooling initiated extensive change in the landscape of east-central Alberta. The flooding of shallow lake basins continued and peaked between about 5700 and 4500 cal. yr BP (Schweger and Hickman 1989). At Moore Lake, birch-spruce forest replaced grassland by about 7000 cal. yr BP (Hickman and Schweger 1996), and there was an increase in the abundance of boreal taxa at Lofty Lake (Lichti-Federovich 1970). The limit of peatland distribution shifted south concurrently with the expansion of the boreal forest and was located somewhere between Mariana lake and Lofty lake 6000 cal. yr BP (Halsey *et al.* 1998). Large-scale paludification of the Mariana lake peatland began about 6800 cal. yr BP (Nicholson and Vitt 1990), accompanied by a marked increase of *Sphagnum* spores in the pollen record (Hutton *et al.* 1994).

At Athabasca, peat expanded outwards from the original nucleation sites between 7000 and 5000 cal. yr BP. The lateral expansion of these initially monocot-dominated communities was driven by rising water tables that led to flooding and paludification of surrounding uplands. Peat buildup was more rapid in the northern bog basin than in the present-day treed fen area. By 6210 cal. yr BP, coresite 15 was occupied by a monocot fen. At about the same time, peat built up to the level of the outflow channel that connects the northern bog and southern fen basins. The shrubby fen present in zone 1 of core 16 was invaded by bryophytes, and subsequent community succession indicates rapid acidification and transition from rich fen to poor fen or bog (Figure 2.12d).

In the southern fen basin, peat first initiated around 6000 cal. yr BP. The steep sides of the basin and gentle landscape gradient towards the south / south-west channel water along the deepest route, which underlies coresites 17, 7 and 11 (Figures 2.2; 2.5). This channel probably carried water at least seasonally throughout the Holocene,

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

and marshes may have been present along some of its length. By 6020 cal. yr BP, water levels were stable enough to support a monocot-dominated peatland community at the southern end of the fen (coresite 11). This site is located just north of a topographic constriction where two upland outcrops converge into the fen channel. Once peat began accumulating, drainage was impeded and paludification progressed rapidly upstream, reaching coresite 7 about 5280 cal. yr BP. At the same time, peat failed to expand from coresite 11 to coresite 12 only 100 meters farther west, presumably because of steeper substrate gradients in this direction.

5000 - 3000 cal. yr BP

Between 5000 and 3000 cal. yr BP, modern vegetation became established in most of east-central Alberta. The remaining shallow lake basins filled during this period, and by about 3200 cal. yr BP climate was essentially modern (Schweger and Hickman 1989). Southern boreal forest was present at Moore Lake (Hickman and Schweger 1996), and modern flora established at Lofty Lake about 3800 cal. yr BP (Lichti-Federovich 1970). The limit of peatland distribution continued to expand southwards (Zoltai and Vitt 1990; Halsey *et al.* 1998). The pollen record at Mariana Lake suggests regional expansion of *Sphagnum* peatlands (Hutton *et al.* 1994), and basal dates from the adjacent peatland indicate that the entire drainage path presently occupied by the site was accumulating peat by about 3100 cal. yr BP (Nicholson and Vitt 1990).

At Athabasca, most of the southern fen basin paludified between 5000 and 3000 cal. yr BP (Figure 2.15). By 4640 cal. yr BP, peat was accumulating at coresite 17. Coresite 4 at the northern edge of the fen was paludified by about 2990 cal. yr BP. Throughout this period of rapid expansion, the fen basin was occupied by a monocot-dominated rich fen community. Upslope expansion was most likely driven by an overall rise in the peatland water table resulting from impeded drainage throughout the lower parts of the basin. The high rates of peat accumulation observed in the northern

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

part of the fen (especially cores 2, 4, 7 and 17; Table 2.1) presumably resulted from rapidly rising water tables. Cores taken closer to the fen margin show lower vertical accumulation rates, which could reflect lower or less stable water levels. Alternatively, peat accumulation at some marginal sites may pre-date the arrival of the expanding fen. The environmental reconstruction for core 3 (Figure 2.12b) suggests that peat accumulation began under relatively dry conditions thay may have limited vertical accumulation rates.

3000 cal. yr BP - present

The southern limit of the boreal forest and modern limit of peatland distribution were established in Alberta by 3000 cal. yr BP. Climate and vegetation were essentially modern from this time onwards and no new peatlands formed south of the distributional limit (Halsey *et al.* 1998). Farther north, new sites originated and existing peatlands continued to expand. At Mariana Lake, the main period of expansion had probably passed by 3000 cal. yr BP, and subsequent development involved mainly landform differentiation and ombrotrophication (Nicholson and Vitt 1990). At Athabasca, paludification continued, but its focus shifted from the large basins towards the western and north-western regions of the site.

The small number of basal dates from regions outside the main basins complicates reconstruction of peatland development in these shallow (mostly < 150 cm) areas. Cores that were examined (Figure 2.8c) originated less than 3000 years ago by *Sphagnum* invasion of upland forest. The basal section of core 10 suggests that fire may have played a key role in peatland initiation in these areas. A relationship between fire and the paludification of upland forest has been observed several decades ago (e.g. Lukkala 1933; Huikari 1956), and is usually attributed to a temporary rise in local water tables following a burn (Korhola 1992; 1995). Alternatively, the relatively recent paludification of these areas may be linked to changes in regional hydrology that resulted from peat accumulation, or to the attainment of modern climatic conditions.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Factors controlling peatland expansion

The results of this study suggest that peatland development at Athabasca was controlled by multiple allogenic and autogenic factors that often acted synergistically to produce the patterns of landscape succession observed. Peat initiated in response to regional climatic change at the end of the early Holocene warm period. Subsequent site expansion, however, was asynchronous and followed a pattern that suggests strong local environmental control. The rapid paludification of the southern fen basin, for example, was most likely triggered by impeded drainage resulting from peat buildup further downslope. Such 'back-paludification' has been observed by other workers (Korhola 1996; Charman 1994; Gauhl 1991; Foster and King 1984; Foster and Fritz 1987) and demonstrates that presence of peat on a landscape can raise local or even regional water tables and promote further peatland development (Kulczynski 1949; Heinselman 1970; Ivanov 1981).

Given the dependence of peatlands on seasonally stable water tables (Zoltai and Vitt 1990) a relationship between topography and rates of peat expansion (Korhola 1994; 1992; Almquist-Jacobson and Foster 1995; Mäkilä 1997) is to be expected. This is particularly true in continental areas where peatlands are more dependent on local ground- and surface water systems than in oceanic regions (Kulczynski 1949; Glaser *et al.* 1997). Effects of topography on rates of lateral expansion cannot be quantified in this study because the peat surface was not levelled and precise slope gradients of the underlying mineral terrain are unknown. The large basins identified by the depth reconstruction, however, are real topographic depressions, and early peat expansion in the open fen area was apparently limited by the steep marginal slopes of the basin. Peat on these slopes only initiated after accumulation in the central areas of the basin had sufficiently raised peatland water tables, causing the flooding of marginal forest areas.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

The relationship between vertical peat accumulation and lateral expansion needs to be explored further. Field evidence indicates that the majority of lateral site expansion often occurs while a site is still minerotrophic, even if it subsequently develops into a raised bog (Korhola 1992; Korhola 1994; Almquist-Jacobson and Foster 1995; Ikonen 1993). In the large peatland complexes of continental regions, fens cover large areas of land with gentle topographic gradients and bogs are usually underlain by fen deposits. Most current models of peatland development (Clymo 1984; Winston 1994; Almquist-Jacobson and Foster 1995) describe the dynamics of raised bogs. In order to understand the lateral expansion of peatlands, we need models that include fen development.

Paludification by *Sphagnum* invasion into upland forest has been described from Finland (Cajander 1913; Aario 1932; Tolonen 1967; Hulme 1994), Estonia (Zobel 1990), and Alaska (Heilman 1966; Ugolini and Mann 1979; Klinger 1996). Cajander (1913) attributed this type of paludification primarily to *S. acutifolium* (= *S. capillifolium*), with the importance of *S. fuscum* increasing in northern areas. Other studies (Aario 1932; Noble *et al.* 1984) point towards *S. girgensohnii* as the key species involved. *Sphagnum girgensohnii* is characteristic of shaded coniferous forest (Vitt and Andrus 1977) but was not recovered from any cores in this study. However, basal samples from cores in this group were often poorly preserved, and stem cortices required for reliable identification of *S. girgensohnii* were rarely present. Thus, there is a possibility that *S. girgensohnii* was missed in some basal samples.

The nature of the plant communities throughout most of the western and north-western treed fen and bog regions suggests that the site is still expanding. In some areas, however, water levels are low and apparently unstable. These regions are likely to be extremely sensitive to changes in the regional moisture balance. Shallow peat deposits are extensive throughout continental western Canada, and factors that control their origin and persistence seem worthy of future attention.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Patterns of vegetation succession

The results of this study point towards strong physiographic control over both peatland initiation and subsequent patterns of vegetation succession. Sites that originated wet and minerotrophic have a tendency to eventually be colonized by *Sphagnum*, as predicted by classic models of peatland development (Weber 1908). This trend seems to be most pronounced in basins with little or no water movement (coresites 16 and 18). Sphagna have recently begun to colonize the marginal areas of the open fen, but species present so far are characteristic of moderate-rich fen conditions, and most areas show no evidence for a development towards ombrotrophy. In the central region of the fen basin where water flow is most pronounced, vegetation has remained essentially unchanged since the beginning of peat formation. It is these central areas where peat accumulation has been most rapid, and the upslope expansion of the fen has caused reverse successional sequences in some marginal sites.

Vertical peat accumulation rates

Differences in vertical peat accumulation rates among cores and their apparent link to local moisture availability are among the most surprising results of this study. Within-site variability in long-term apparent rates of peat accumulation has been observed previously (Korhola 1992; 1996; Korhola *et al.* 1995b; Foster and King 1984; Almquist-Jacobson and Foster 1995; Mäkilä 1997; Ikonen 1993). Many of these studies, however, are restricted to a single peatland type, and few workers have systematically compared long-term peat accumulation between landforms of the same site. Furthermore, observed differences are often hard to interpret because factors such as temporal changes in accumulation or mass loss in the catotelm cannot be accounted for by apparent rates (see e.g. Robinson and Moore 1999; Clymo *et al.* 1998).

Based on regional comparisons, bogs are generally thought to accumulate peat (or carbon) faster than fens (Tolonen *et al.* 1992; Korhola *et al.* 1995b). Robinson and

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Moore (1999) compared apparent rates of peat accumulation over the last 1200 years in a peatland located in the discontinuous permafrost zone near Fort Simpson (Northwest Territories) and found faster accumulation in poor fen and ombrotrophic bog sites than in rich fen, peat plateau and collapse fen. Malmer (1986) suggested that the succession from fen to bog is accompanied by increasing rates of peat accumulation, and Thormann *et al.* (1999b) calculated higher carbon accumulation potentials in *Sphagnum*-dominated peatlands than in brown-moss or graminoid-dominated systems.

At Athabasca, peat accumulation has been fastest in the rich fen area. This supports the notion of Kulczynski (1949) that fen communities can promote and successfully track gradual increases in local water tables, at least within certain physiographic contexts. The results contradict the idea that fens have inherently low peat accumulation potential. The slow rates of accumulation observed in drier (*Sphagnum* - dominated) regions could be the result of greater susceptibility of these areas to fire (Kuhry 1994). Alternatively, they could be indicative of low actual (*sensu* Clymo *et al.* 1998) rates of peat accumulation resulting from moisture limitation, as postulated by Robinson and Moore (1999) for their study area in the Northwest Territories.

Overall, this study presents a highly dynamic picture of peatland development. Climate, physiography, and peat accumulation have all played important and often interacting roles in causing the sequence of events observed. As noted by Heinselman (1970), the result is not a stable, uniform landscape, but rather a diverse mosaic of different landform types. The sensitivity of each of these landforms to environmental change is likely to differ, with individual responses depending on both peatland type and the relative stability of hydrological conditions that support local peat accumulation.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

LITERATURE CITED

Aaby B and Berglund BE. 1986. Characterization of peat and lake deposits. Pages 231-246 in: Berglund BE. (editor). *Handbook of Holocene Palaeoecology and Palaeohydrology*. John Wiley & Sons Ltd. Chichester.

Aario L. 1932. Pflanzentopographische und paläogeographische Mooruntersuchungen in N-Satakunta. *Fennia* 55:1-179.

Adams GD. 1988. Wetlands of the Prairies of Canada. Pages 155-198 in: National Wetlands Working Group. *Wetlands of Canada*. Sustainable Development Branch, Environment Canada, Ottawa, Ontario, and Polyscience Publications Inc., Montréal, Québec.

Almquist-Jacobson H and Foster DR. 1995. Toward an integrated model for raised-bog development: Theory and field evidence. *Ecology* 76:2503-2516.

Anderson LE. 1990. A checklist of *Sphagnum* in North America north of Mexico. *The Bryologist* 93:500-501.

Anderson LE, Crum HA and Buck WR. 1990. List of the mosses of North America north of Mexico. *The Bryologist* 93:448-499.

Andrejko MJ, Fiene F and Cohen AD. 1983. Comparison of ashing techniques for determination of the inorganic content of peats. Pages 5-20 in: Jarrett PM. (editor). *Testing of Peats and Organic Soils*. Americal Society for Testing and Materials.

Birks HJB. 1986. Numerical zonation, comparison and correlation of Quaternary pollen-stratigraphical data. Pages 743-774 in: Berglund BE. (editor). *Handbook of Holocene Palaeoecology and Palaeohydrology*. John Wiley & Sons Ltd., Chichester.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Birks HJB, Line JM, Juggins S, Stevenson AC and ter Braak CJF. 1990. Diatoms and pH reconstruction. *Philosophical Transactions of the Royal Society of London B* 327:263-278.

Brugam RB and McCance Johnson S. 1997. Holocene lake-level rise in the Upper Peninsula of Michigan, USA, as indicated by peatland growth. *The Holocene* 7:355-359.

Cajander AK. 1913. Studien über die Moore Finnlands. *Acta Forestalia Fennica* 2. 298pp.

Canadian Climate Program. 1993. *Canadian Climate Normals 1961-1990.* Environment Canada, Atmospheric Environment Service.

Charman DJ. 1994. Patterned fen development in northern Scotland: developing a hypothesis from palaeoecological data. *Journal of Quaternary Science* 9:285-297.

Chee W-L and Vitt DH. 1989. The vegetation, surface water chemistry and peat chemistry of moderate-rich fens in central Alberta, Canada. *Wetlands* 9:227-262.

Clymo RS. 1983. Peat. Pages159-224 in: Gore AJP. editor. *Mires: swamp, bog, fen and moor; General studies*. Ecosystems of the World 4A. Elsevier Scientific Publishing Company. Amsterdam.

Clymo RS. 1984. The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London B* 303:605-654.

Clymo RS, Turunen J and Tolonen K. 1998. Carbon accumulation in peatland. *Oikos* 81:368-388.

Damman WH. 1979. Geographic patterns in peatland development in eastern North America. Pages 42-57 in: *Proceedings of the International Symposium on*

Classification of Peat and Peatlands. International Peat Society. Hyytiälä, Finland

Dargie TCD. 1984. On the integrated interpretation of indirect site ordinations: a case study using semi-arid vegetation in southeastern Spain. *Vegetatio* 55:37-55.

Deutsch CV and Journel AG. 1998. *GSLIB. Geostatistical Software Library and User's Guide*. Oxford University Press. New York.

Dufrêne M and Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-366.

Dyke AS and Prest VK. 1987. *Paleogeography of northern North America, 18000 - 5000 years ago*. Geological Survey of Canada map 1703A, scale 1:12,500,000.

Ecological Stratification Working Group. 1996: *A national ecological framework for Canada.* Report and national map at 1:750000 scale. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch. Ottawa / Hull.

Eurola S. 1962. Über die regionale Einteilung der südfinnischen Moore (Suomalaisen Eläin-ja Kasvitieteellisen Seuran Vanamon Kasvitieteelisiä Julkaisuja). *Annales Botanici Societatis Zoologicae Botanicae Fennicae 'Vanamo'* 33:1-243.

Foster DR and Fritz SC. 1987. Mire development, pool formation and landscape processes on patterned fens in Dalarna, Central Sweden. *Journal of Ecology* 75:409-437.

Foster DR and Glaser PH. 1986. The raised bogs of south-eastern Labrador, Canada: Classification, distribution, vegetation and recent dynamics. *Journal of Ecology* 75:47-71.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Foster DR and Wright HEJr. 1990. Role of ecosystem development and climate change in bog formation in central Sweden. *Ecology* 71:450-463.

Foster DR and King GA. 1984. Landscape features, vegetation and developmental history of a patterned fen in south-eastern Labrador, Canada. *Journal of Ecology* 72:115-143.

Gauhl F. 1991. Untersuchungen zur Entwicklung des Schwarzen Moores in der Rhön: Verlauf und Ursachen der Vermoorung. *Flora* 185:1-16.

Gignac LD, Halsey LA and Vitt DH. 2000. A bioclimatic model for the distribution of *Sphagnum*-dominated peatlands in North America under present climatic conditions. *Journal of Biogeography* 27:1139-1151.

Gignac LD, Vitt DH, Zoltai SC and Bayley SE. 1991. Bryophyte response surfaces along climatic, chemical, and physical gradients in peatlands of western Canada. *Nova Hedwigia* 53:27-71.

Glaser PH and Janssens JA. 1986. Raised bogs in eastern North America: transitions in landforms and gross stratigraphy. *Canadian Journal of Botany* 64:395-415.

Glaser PH, Siegel DI, Romanowicz EA and Shen YP. 1997. Regional linkages between raised bogs and the climate, groundwater, and landscape of north-western Minnesota. *Journal of Ecology* 85:3-16.

Gorham E. 1991. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* 1:182-195.

Halsey LA, Vitt DH and Bauer IE. 1998. Peatland initiation during the Holocene in Continental Western Canada. *Climatic Change* 40:315-342.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Harrison SP and Metcalfe SE. 1985. Variations in Lake Levels during the Holocene in North America: an indicator of changes in atmospheric circulation patterns *Géographie physique et Quaternaire* 39:141-150.

Heilman PE. 1966. Change in distribution and availability of nitrogen with forest succession on north slopes in interior Alaska. *Ecology* 47:825-831.

Heinselman ML. 1970. Landscape evolution, peatland types and the environment in the Lake Agassiz Peatlands Natural Area, Minnesota. *Ecological Monographs* 40:235-261.

Hickman M and Schweger CE. 1996. The Late Quaternary palaeoenvironmental history of a presently deep freshwater lake in east-central Alberta, Canada and palaeoclimate implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 123:161-178.

Hill MO and Gauch HG Jr. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42:47-58.

Huikari O. 1956. Primmäärisen soistumisen osuudesta Suomen soiden synnyssä (Untersuchungen über den Anteil der primären Versumpfung an der Entstehung der Finnischen Moore). *Communicationes Instituti Forestalis Fenniae* 46:1-79.

Hulme PD. 1994. A palaeobotanical study of paludifying forest on the island of Hailuoto, northern Finland. *New Phytologist* 126:153-162.

Hutton MJ, MacDonald GM and Mott RJ. 1994. Postglacial vegetation history of the Mariana Lake region, Alberta. *Canadian Journal of Earth Sciences* 31:418-425.

Ikonen L. 1993. Holocene development and peat growth of the raised bog Pesänsuo in southwestern Finland. *Geological Survey of Finland Bulletin* 370:1-58.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Isaaks EH and Srivastava RM. 1989. *An Introduction to Applied Geostatistics*. Oxford University Press. Oxford.

Ivanov KE. 1981. *Water Movement in Mirelands*. Acadamic Press. London.

Janssens JA, Hansen BCS, Glaser PH and Whitlock C. 1992. Development of a raised-bog complex. Pages 189-221 in: Wright HE Jr, Coffin BA and Aaseng NE. (editors). *The patterned peatlands of Minnesota*. University of Minnesota Press. Minneapolis.

Journel AG and Huijbregts ChJ. 1978. *Mining Geostatistics*. Academic Press. London.

Kjearsgaard AA. 1972. *Reconnaissance Soil Survey of the Tawatinaw Map Sheet (83-I)*. Alberta Institute of Pedology Report No. S-72-29. University of Alberta.

Klinger LF. 1996. Coupling of soil and vegetation in peatland succession. *Arctic and Alpine Research* 28:380-387.

Klinger LF and Short SK. 1996. Succession in the Hudson Bay Lowland, northern Ontario, Canada. *Arctic and Alpine Research* 28:172-183.

Korhola A. 1992. Mire induction, ecosystem dynamics and lateral extension on raised bogs in the southern coastal area of Finland. *Fennia* 170:25-94.

Korhola A. 1995. Holocene climatic variations in southern Finland reconstructed from peat-initiation data. *The Holocene* 5:43-58.

Korhola A. 1996. Initiation of a sloping mire complex in southwestern Finland: Autogenic versus allogenic controls. *Écoscience* 3:216-222.

Korhola AA. 1994. Radiocarbon evidence for rates of lateral expansion in raised mires in southern Finland. *Quaternary Research* 42:299-307.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Korhola A, Alm J, Tolonen K, Turunen J and Jungner H. 1995a. Three-dimensional reconstruction of carbon accumulation and CH_4 emission during nine millennia in a raised mire. *Journal of Quaternary Science* 11:161-165.

Korhola A, Tolonen K, Turunen J and Jungner H. 1995b. Estimating long-term carbon accumulation rates in boreal peatlands by radiocarbon dating. *Radiocarbon* 37:575-584.

Kubiw H, Hickman M and Vitt DH. 1989. The developmental history of peatlands at Muskiki and Marguerite Lakes, Alberta (Canada). *Canadian Journal of Botany* 67:3534-3544.

Kuhry P. 1994. The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. *Journal of Ecology* 82:899-910.

Kuhry P, Nicholson BJ, Gignac LD, Vitt DH and Bayley SE. 1993. Development of *Sphagnum* dominated peatlands in boreal continental Canada. *Canadian Journal of Botany* 71:10-22.

Kulczynski MSt. 1949. Torfowiska Polesia: Peat bogs of Polesie. *Mémoires de l'Académie Polonaise des Sciences et des Lettres. Classe des Sciences Mathématiques et Naturelles Serie B: Sciences Naturelles* 15:1-356.

Lavoie M and Richard PJH. 2000. The role of climate on the developmental history of Frontenac Peatland, southern Québec. *Canadian Journal of Botany* 78:668-684.

Lichti-Federovich S. 1970. The pollen stratigraphy of a dated section of Late Pleistocene lake sediment from central Alberta. *Canadian Journal of Earth Sciences* 7:938-945.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Lukkala OJ. 1933. Tapahtuuko nykyisin metsämaan soistumista (Vollzieht sich gegenwärtig Versumpfung von Waldboden). *Communicationes ex Instituto Quaestionum Forestalium Finlandiae* 19:1-127.

Mäkilä M. 1997. Holocene lateral expansion, peat growth and carbon accumulation on Haukkasuo, a raised bog in southeastern Finland. *Boreas* 26:1-14.

Malmer N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. *Canadian Journal of Botany* 64:375-383.

McCune B and Mefford MJ. 1999. *PC-ORD. Multivariate Analysis of Ecological Data*, Version 4. MjM Software Design. Gleneden Beach, Oregon, USA.

Moss EH. 1983. *Flora of Alberta*. University of Toronto Press. Toronto.

Nicholson BJ and Gignac LD. 1995. Ecotope dimensions of peatland bryophyte indicator species along gradients in the Mackenzie River Basin, Canada. *The Bryologist* 98:437-451.

Nicholson BJ and Vitt DH. 1990. The paleoecology of a peatland complex in continental western Canada. *Canadian Journal of Botany* 68:121-138.

Nicholson BJ and Vitt DH. 1994. Wetland development at Elk Island National Park, Alberta, Canada. *Journal of Paleolimnology* 12:19-34.

Noble MG, Lawrence DB and Streveler GP. 1984. *Sphagnum* invasion beneath an evergreen forest canopy in southeastern Alasaka. *The Bryologist* 87:119-127.

Olsson IU. 1986: Radiometric dating. Pages 273-312 in: Berglund, BE. (editor). *Handbook of Holocene palaeoecology and palaeohydrology*. John Wiley & Sons Ltd, Chichester

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Payette S. 1988. Late-Holocene development of subarctic ombrotrophic peatlands: allogenic and autogenic succession. *Ecology* 69:516-531.

Ritchie JC. 1976. The late-Quaternary vegetational history of the western interior of Canada. *Canadian Journal of Botany* 54:1793-1818.

Ritchie JC and Harrison SP. 1993. Vegetation, lake levels, and climate in Western Canada during the Holocene. Pages 401-414 in: Wright HE, Kutzbach JE, Webb T III, Ruddiman WF, Street-Perrott FA and Bartlein PJ. (editors). *Global Climates since the Last Glacial Maximum.* University of Minnesota Press. Minneapolis.

Robinson SD and Moore TR. 1999. Carbon and peat accumulation over the past 1200 years in a landscape with discontinuous permafrost, northwestern Canada. *Global Biogeochemical Cycles* 13:591-601.

Rowe RS. 1972. *Forest Regions of Canada.* Canadian Forest Service Publication No. 1300. Department of the Environment, Ottawa.

Schweger CE and Hickman M. 1989. Holocene paleohydrology of central Alberta: testing the general-circulation-model climate simulations. *Canadian Journal of Earth Sciences* 26:1826-1833.

Sjörs H. 1980. An arrangement of changes along gradients, with examples from successions in boreal peatlands. *Vegetatio* 43:1-4.

Sjörs H. 1983. Mires of Sweden. Pages 69-94 in: Gore AJP. (editor). *Mires: swamp, bog, fen and moor: Regional studies* . Ecosystems of the World 4B. Elsevier Scientific Publishing Company. Amsterdam

Stuiver M and Reimer PJ. 1993. Extended ^{14}C database and revised CALIB radiocarbon calibration program. *Radiocarbon* 35: 215-230.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Stuiver M, Reimer PJ, Bard E, Beck JW, Burr GS, Hughen KA, Kromer B, McCormac G, van der Plicht J and Spurk M. 1998. INTCAL98 radiocarbon age calibration, 24,000-0 cal BP. *Radiocarbon* 40:1041-1083.

Tallis JH. 1983. Changes in wetland communities. Pages311-347 in: Gore AJP. (editor). *Mires: swamp, bog, fen and moor: General studies* . Ecosystems of the World 4A. Elsevier Scientific Publishing Company. Amsterdam.

Tallis JH. 1991. Forest and moorland in the South Pennine uplands in the mid-Flandrian period: III. The spread of moorland - local, regional and national. *Journal of Ecology* 79:409-415.

Tallis JH and Switsur VR. 1990. Forest and moorland in the South Pennine uplands in the mid-Flandrian period: II. The hillslope forests. *Journal of Ecology* 78:857-883.

Tarnocai C, Adams GD, Glooschenko V, Glooschenko WA, Grondin P, Hirvonen HE, Lynch-Stewart P, Mills GF, Oswald ET, Pollett FC, Rubec CDA, Wells ED and Zoltai SC. 1988: Appendix I: The Canadian Wetland Classification System. Pages 413-427 in: National Wetlands Working Group, *Wetlands of Canada.* Sustainable Development Branch, Environment Canada. Ottawa, Ontario, and Polyscience Publications Inc. Montréal, Québec.

ter Braak CJF. 1995. Ordination. Pages 91-173 in: Jongman RHG, ter Braak CJF and van Tongeren OFR. (editors). *Data Analysis in Community and Landscape Ecology.* Cambridge University Press. Cambridge.

ter Braak CJF and Barendregt LG. 1986. Weighted averaging of species indicator values: its efficiency in environmental calibration. *Mathematical Biosciences* 78:57-72.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Thormann MN, Currah RS and Bayley SE. 1999a. The mycorrhizal status of the dominant vegetation along a peatland gradient in southern Boreal Alberta, Canada. *Wetlands* 19:438-450.

Thormann MN, Szumigalski AR and Bayley SE. 1999b. Aboveground peat and carbon accumulation potentials along a bog-fen-marsh wetland gradient in southern boreal Alberta, Canada. *Wetlands* 19:305-317.

Tolonen K. 1967. Über die Entwicklung der Moore im finnischen Nordkarelien. *Annales Botanici Fennici* 4:219-416.

Tolonen K, Vasander H, Damman AWH and Clymo RS. 1992. Rate of apparent and true carbon accumulation in boreal peatlands. Pages319-333 in: *Proceedings of the 9th International Peat Congress*. Uppsala, Sweden.

Turunen J, Tomppo E, Tolonen K and Reinikainen A. 2002. Estimating carbon accumulation rates of undrained mires in Finland - application to boreal and subarctic regions. *The Holocene* 12:69-80.

Ugolini FC and Mann DH. 1979. Biopedological origin of peatlands in South East Alaska. *Nature* 281:366-368.

Vance RE, Beaudoin AB and Luckman BH. 1995. The paleoecological record of 6 ka BP climate in the Canadian Prairie Provinces. *Géographie physique et Quaternaire* 49:81-98.

Vitt DH. 1994. An overview of factors that influence the development of Canadian peatlands. *Memoirs of the Entomological Society of Canada* 169:7-20.

Vitt DH and Andrus RE. 1977. The genus *Sphagnum* in Alberta. *Canadian Journal of Botany* 55:331-357.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Vitt DH, Halsey LA, Bauer IE and Campbell C. 2000. Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. *Canadian Journal of Earth Sciences* 37:683-693.

Ward JH. 1963. Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* 58:236-244.

Weber CA. 1908. Aufbau und Vegetation der Moore Norddeutschlands. *Englers Botanische Jahrbücher Beiblatt.* 90:19-34.

Winston RB. 1994. Models of the geomorphology, hydrology, and development of domed peat bodies. *Geological Society of America Bulletin* 106:1594-1604.

Wynnyk A, Lindsay JD, Heringa PK and Odynsky W. 1964. *Exploratory Soil Survey of Alberta Map Sheets 83-O, 83-P, and 73-M.* Preliminary Soil Survey Report 64-1. Research Council of Alberta, Edmonton.

Zobel M. 1990. Soil oxygen conditions in paludifying boreal forest sites. *Suo* 41:81-89.

Zoltai SC, Siltanen RM and Johnson RD. 2000. *A wetland database for the western boreal, subarctic, and arctic regions of Canada.* Information Report NOR-X-368. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre Edmonton, Alberta.

Zoltai SC, Taylor S, Jeglum JK, Mills GF and Johnson JD. 1988. Wetlands of Boreal Canada. Pages 97-154 in: National Wetlands Working Group. *Wetlands of Canada.* Sustainable Development Branch, Environment Canada, Ottawa, Ontario, and Polyscience Publications Inc., Montréal, Québec.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Zoltai SC and Vitt DH. 1990. Holocene climatic change and the distribution of peatlands in western interior Canada. *Quaternary Research* 33:231-240.

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Table 2.1: Minimum variance cluster groups of macrofossil data, and taxa with significant indicator values for each cluster. RA = Relative abundance (% of total abundance of taxon *j* that occurs within cluster *k*). RF = Relative frequency (% of samples in cluster *k* that contain taxon *j*). IV = Indicator value. Only taxa with indicator values >20 are shown

Cluster group	number of samples	indicator species / group	RA (%)	RF (%)	IV	*p*
1	11	robust woody roots	57	100	56.7	0.0001
		Sphagnum warnstorfii	98	45	44.4	0.0001
		Aulacomnium palustre	80	27	21.7	0.0085
2	12	wood / bark	64	100	63.7	0.0001
3	19	*Sphagnum fuscum*	93	100	92.6	0.0001
4	16	*Sphagnum magellanicum*	85	100	84.6	0.0001
		ericaceous roots	31	88	26.8	0.0093
5	34	smooth woody roots	50	71	35.2	0.0015
		dicot leaves	49	65	31.4	0.0015
6	7	*Calliergon giganteum*	97	100	97.4	0.0001
7	26	herbaceous remains	34	100	34.5	0.0001
8	11	*Sphagnum angustifolium*	90	100	90.1	0.0001

A version of this chapter has been submitted for publication.
Bauer IE, Gignac LD and Vitt DH 2002. The Holocene.

Table 2.2: Basal radiocarbon dates and long-term apparent rates of peat accumulation.

core no.	lab no.	depth (cm)	^{13}C (‰)	conventional ^{14}C date (yr BP)	error (SD)	calibrated ^{14}C age (cal. yr BP)	calibrated age range (2)	apparent rate of peat accumulation (mm/year)
1	BGS 1968	85 - 88	-27	1910	110	1850	2115 - 1580	0.47
2	BGS 1969	188 - 192	-27	2460	90	2540	2745 - 2340	0.75
3	BGS 1970	110 - 113	-27	2400	110	2480	2747 - 2168	0.45
4	BGS 1971	216 - 220	-27	2850	110	2990	3274 - 2765	0.73
5	BGS 1972	96 - 99	-27	2160	90	2160	2343 - 1939	0.45
7	BGS 1973	390 - 394	-27	4600	110	5280	5575 - 4957	0.74
8	BGS 1974	186 - 190	-27	3600	120	3900	4247 - 3596	0.48
10	BGS 1976	62 - 68	-27	1650	100	1560	1769 - 1349	0.42
11	BGS 1977	330 - 334	-27	5240	110	6020	6262 - 5756	0.55
12	BGS 1978	200 - 204	-27	3920	120	4340	4802 - 3985	0.47
13	BGS 1979	166 - 170	-27	3470	110	3740	4009 - 3456	0.45
14	BGS 1980	85 - 89	-27	2850	100	2990	3262 - 2768	0.29
15	BGS 1981	226 - 230	-27	5440	120	6210	6434 - 5957	0.37
16	BGS 1982	386 - 390	-27	6540	140	7440	7658 - 7209	0.52
17	BGS 2118	435 - 439	-29.09	4120	100	4640	4861 - 4399	0.94
18	BGS 2119	273 - 277	-29.51	6140	80	7020	7221 - 6795	0.39

Since measured ^{13}C values were not available for most samples, a value of -27 3 ‰ was assumed for peat (see Olsson 1986). Note that the error term influences (increases) the calibrated age range. For further details, see Stuiver and Reimer (1993).

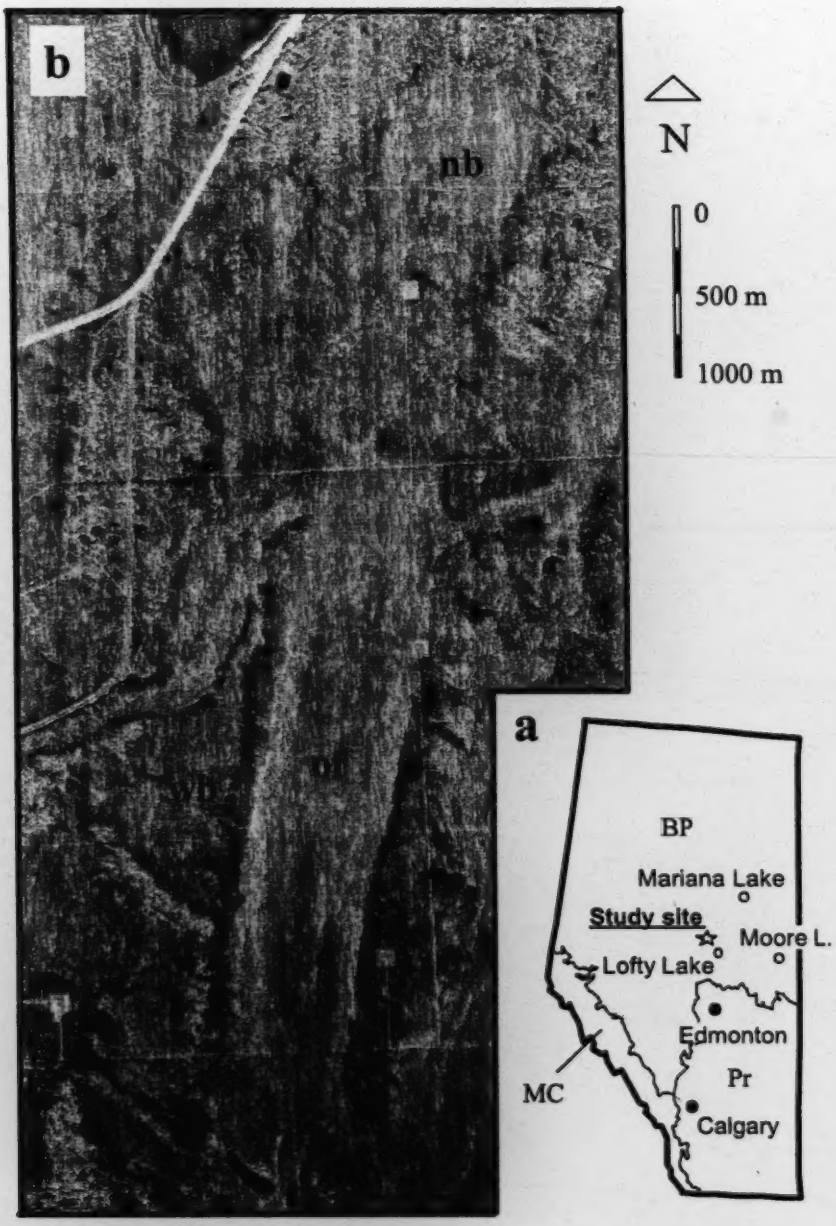


Figure 2.1: **(a)** Location of the study area (star) within Alberta, Canada. Open circles mark location of paleoecological sites mentioned in the text. Lines represent important ecozone boundaries (Ecological Stratification Working Group 1996): BP = Boreal Plains; Pr = prairies; MC = Montane Cordillera. **(b)** Aerial photograph of the Athabasca peatland complex. Letters denote regions referred to in the text: nb = northern bog; wb = western bog; tf = treed fen; of = open fen. Photographs courtesy of Air Photo Distribution, Government of Alberta; reproduced with permission.

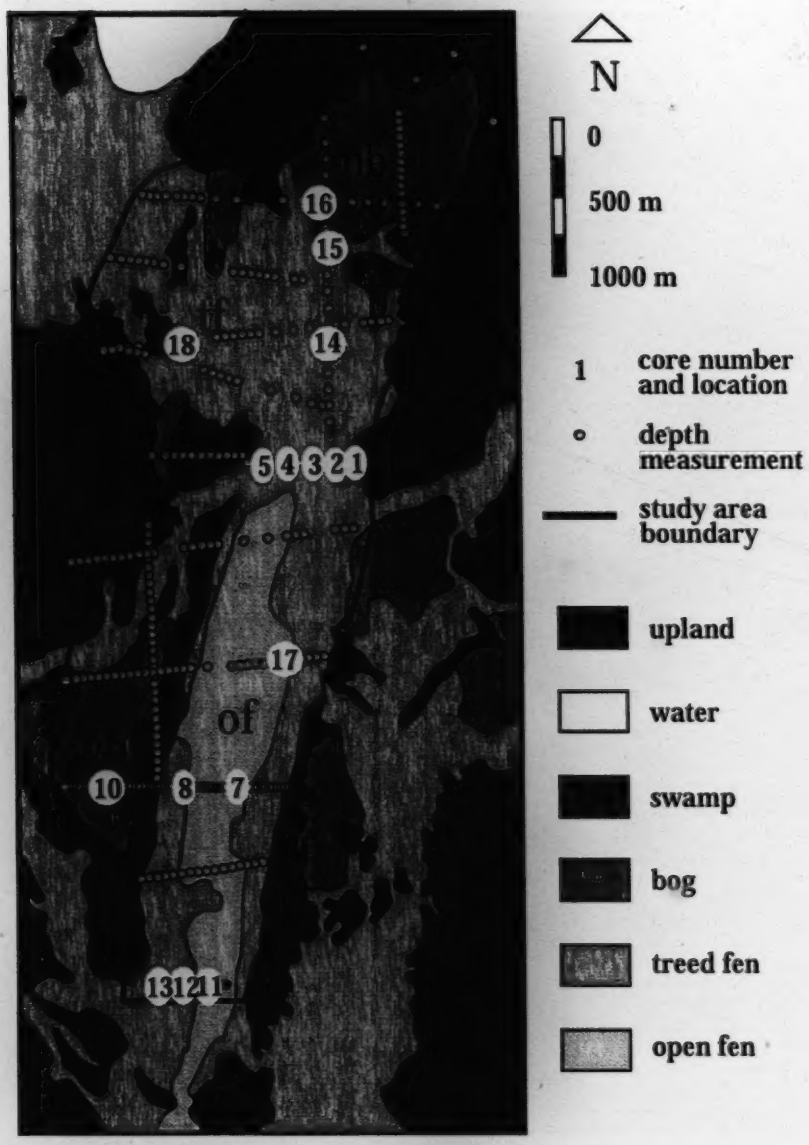


Figure 2.2: Map of the study area, showing main peat landforms, depth survey points with valid measurements, and coring locations. Landforms were mapped from 1:20,000 aerial photographs taken in 1990. (Mapping of wetland classes by L. Halsey; see Appendix 1 for classification used). Letters used to denote regions are the same as in Figure 2.1

Figure 2.3: Landform diversity at the Athabasca peatland complex. **(a)** The open fen area; **(b)** The northern bog. See Figures 2.1 and 2.2 for location of these sites. Both photographs were taken in September 1996.

Figure 2.4: (a) The Macaulay peat sampler. **(b)** basal section of peat core

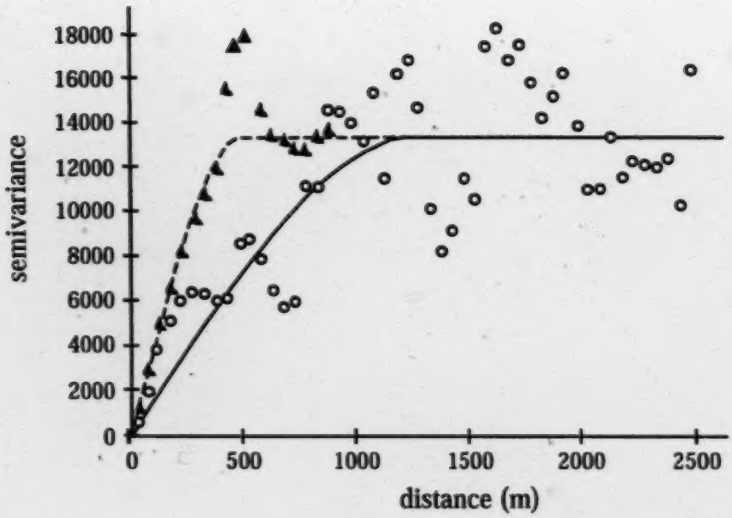


Figure 2.5: Anisotropic variogram model used for spatial interpolation of trend surface residuals. Filled triangles: observed residual semivariance in the direction of least spatial continuity (105 °); open circles: observed residual semivariance in the direction of greatest spatial continuity (15 °). Points for each direction are shown up to the maximum search radius used during interpolation. Broken and solid lines represent the shape of the fitted anisotropic variogram model in both directions. For further explanation, see text.

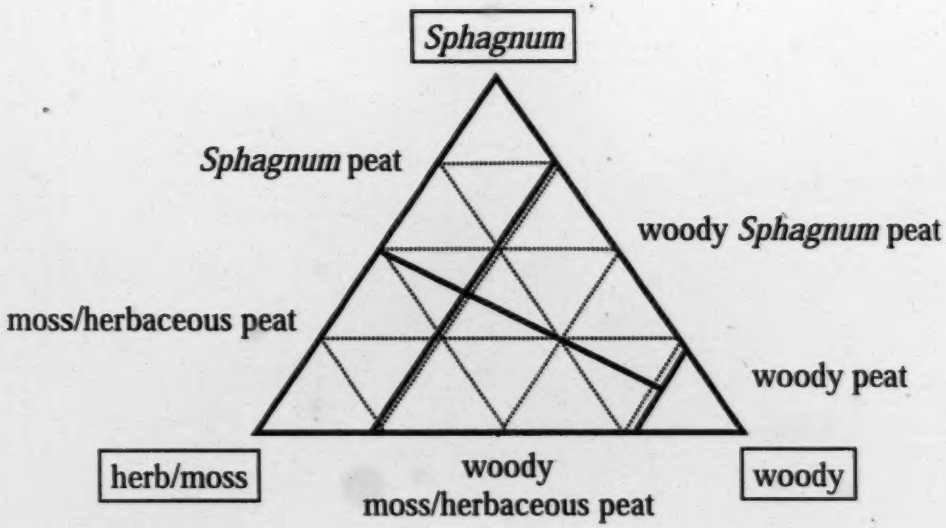


Figure 2.6: Classification used to assign samples to broad peat type categories.Terms in boxes at the three points of the triangle refer to the different types of macrofossil remains scored in each sample (non-*Sphagnum* moss and herbaceous remains were combined). Each of these remains was given a score from zero to four, represented by the solid sides of the triangle and stippled lines. Scores for each sample sum to four, so all possible combinations of scores fall within in a two-dimensional ternary diagram. Solid lines within the triangle separate the five peat type categories used, which are named along the sides of the triangle.

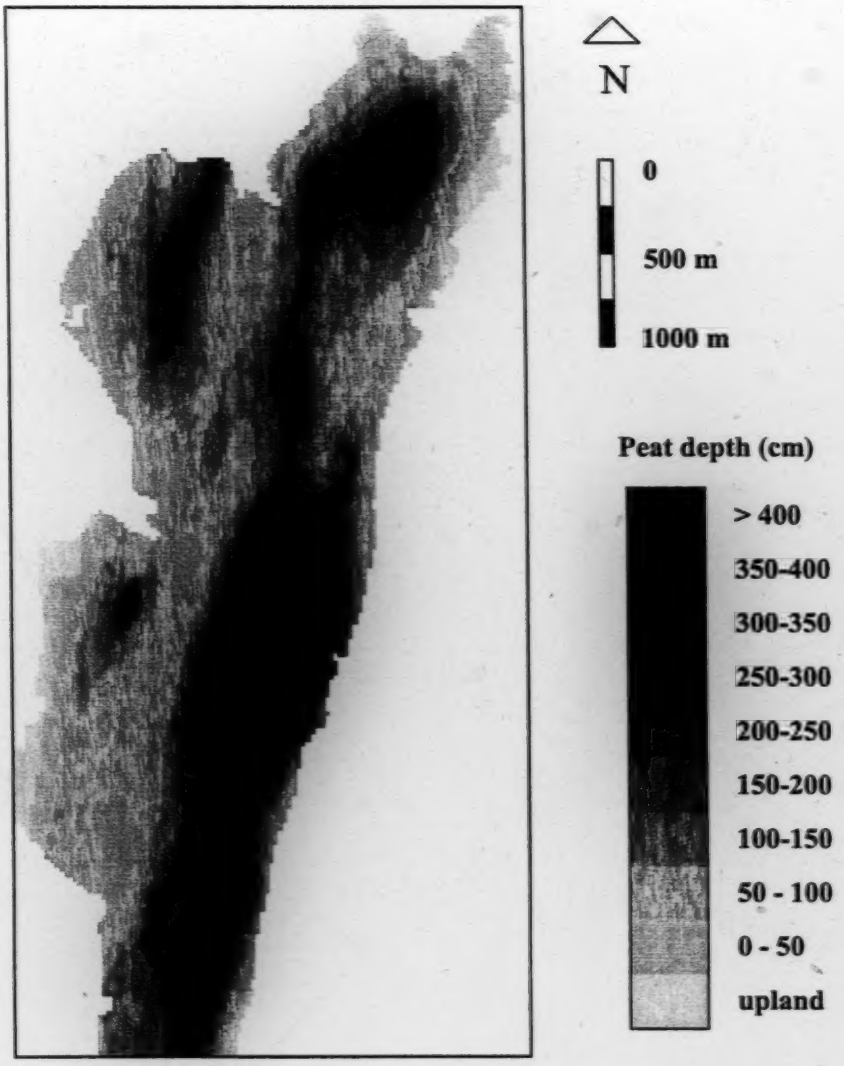


Figure 2.7: Interpolated map of peat depth throughout the study area.

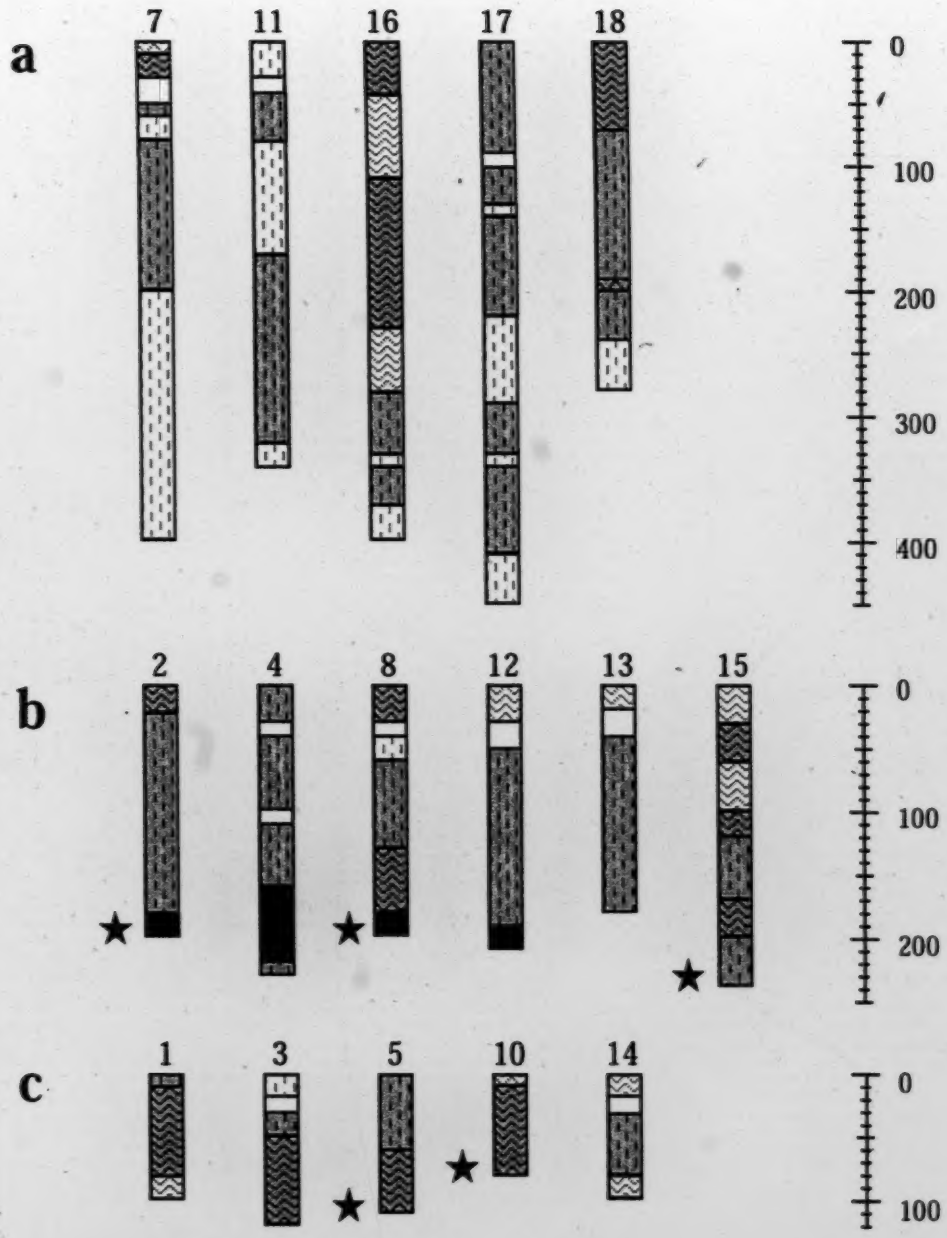


Figure 2.8: Lithology of 16 cores from the study area. Core numbers correspond to those shown in Figure 2.2. *Sphagnum* peat; *Sphagnum* peat with wood; woody peat; moss / herbaceous peat; moss / herbaceous peat with wood; gap in core record. Stars (★) denote cores in which basal peat samples contained at least 3% charcoal

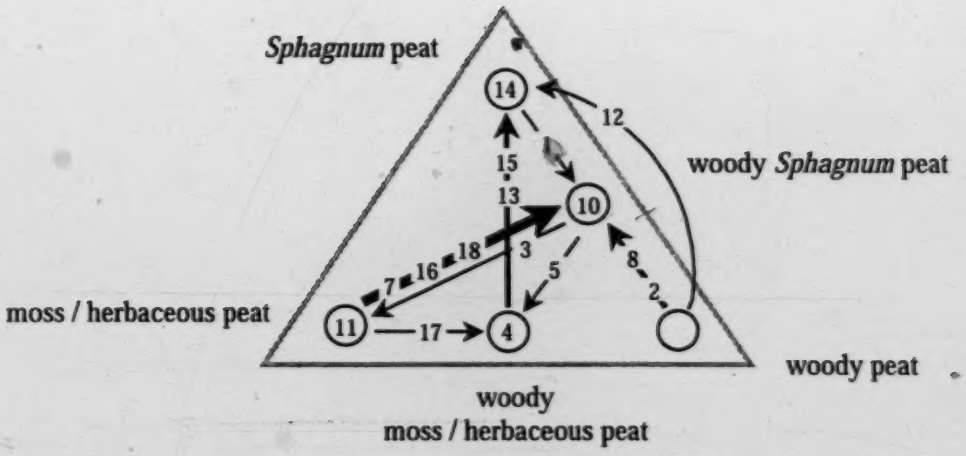


Figure 2.9: Overall successional development of the 16 cores. Open circles represent the five basic peat types named at the sides of the triangle. Arrows connect the basal peat type (based on average scores of two basal macrofossil samples) with the peat type at the surface (based on average scores of uppermost three macrofossil samples). The relative thickness of each arrow denotes the number of cores that follow a given sequence, with the identification numbers of individual cores plotted on each arrow (cf. Figure 2.2). If both basal and surface peat belong to same peat type category, the core number is plotted within the open circle representing that category.

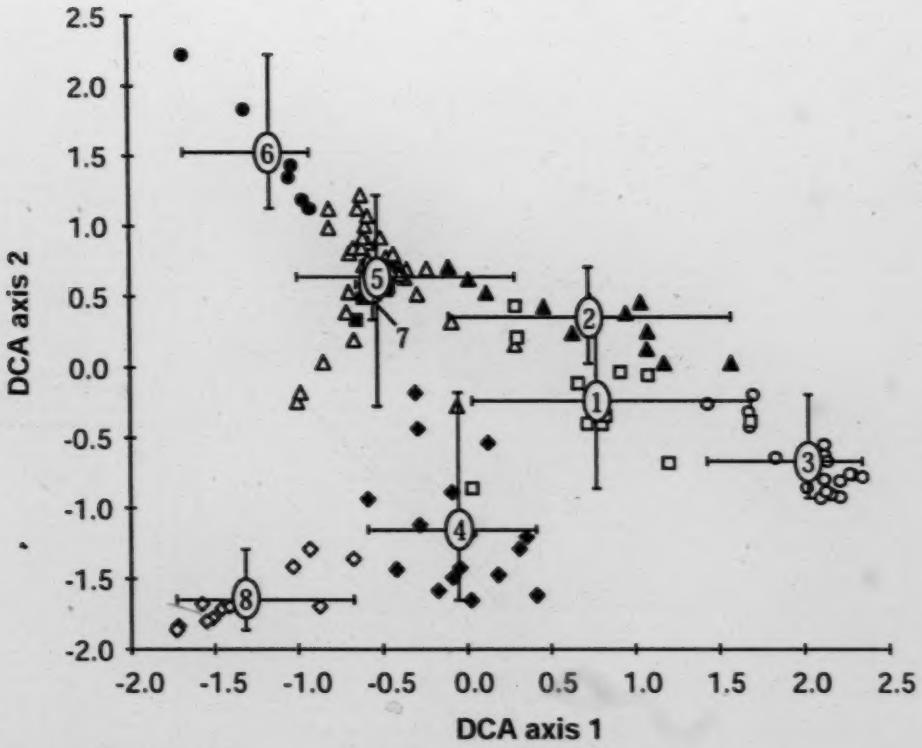


Figure 2.10: DCA Ordination of 136 macrofossil samples. Numbers mark the bivariate mean (centroid) of minimum variance cluster groups, and error bars indicate the range of values on each axis. Symbols and indicator taxa for groups are: (1) □ robust woody roots, *Sphagnum warnstorfii, Aulacomnium palustre*; (2) ▲ wood / bark; (3) ○ *S. fuscum / capillifolium*; (4) ◆ *S. magellanicum*, ericaceous roots; (5) △ smooth woody roots, dicot leaves; (6) ● *Calliergon giganteum*; (7) ■ herbaceous remains; (8) ◇ *S. angustifolium*. For indicator values and significance levels refer to Table 2.1.

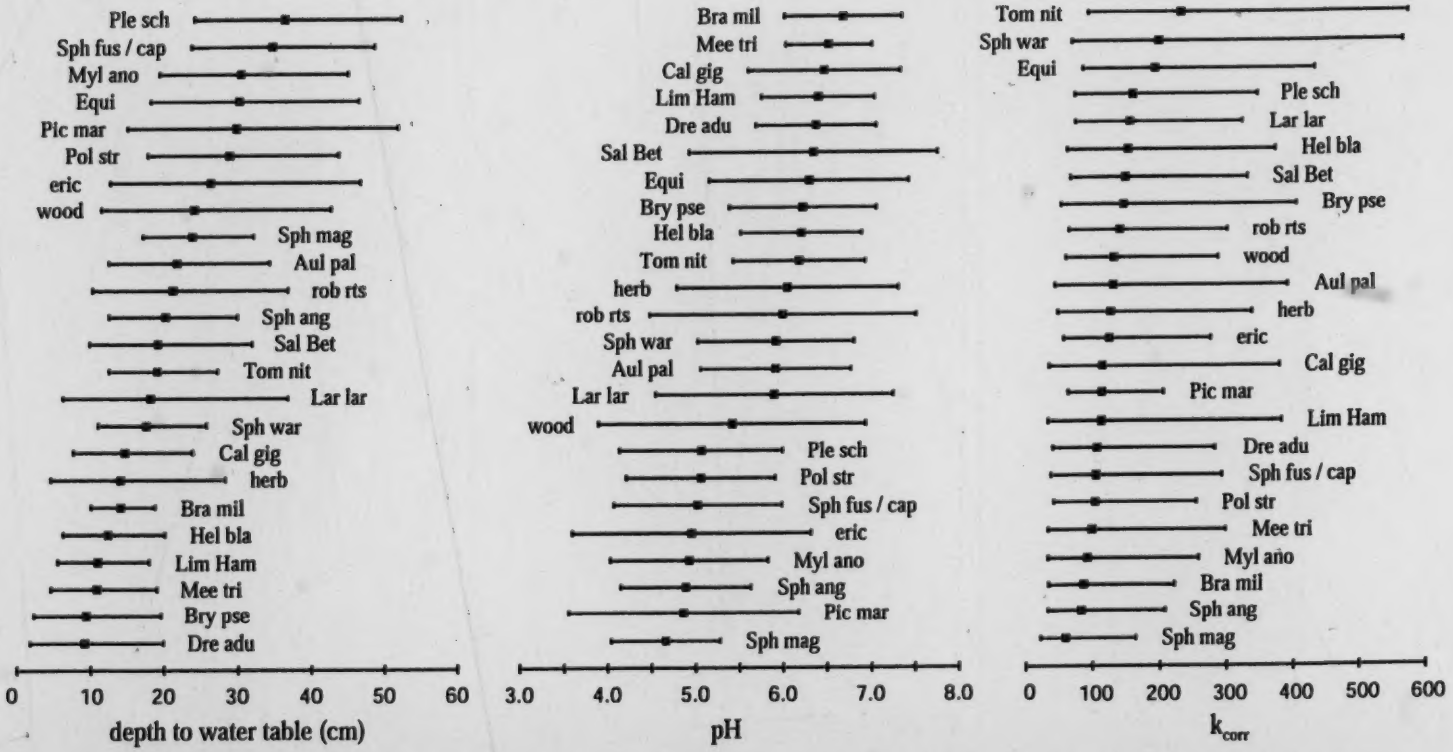


Figure 2.11: Mean indicator values and tolerance ranges of macrofossil taxa for depth to water table, pH, and conductivity corrected for hydrogen ions (kcorr). Aul pal = *Aulacomnium palustre*; Bra mil = *Brachythecium mildeanum*; Bry pse = *Bryum pseudotriquetrum*; Cal gig = *Calliergon giganteum*; Dre adu = *Drepanocladus aduncus*; Equi = *Equisetum* spp.; eric = ericaceous roots; Hel bla = *Helodium blandowii*; herb = herbaceous (monocot) remains; Lar lar = *Larix laricina*; Lim Ham = *Limprichtia revolvens / Hamatocaulis vernicosus* ; Mee tri = *Meesia triquetra*; Myl ano = *Mylia anomala*; Pic mar = *Picea mariana*; Ple sch = *Pleurozium schreberi*; Pol str = *Polytrichum strictum*; rob rts = robust woody roots; Sal Bet = dicot (*Salix* & *Betula*) leaves; Sph ang = *Sphagnum angustifolium*; Sph fus / cap = *Sphagnum fuscum / capillifolium*; Sph mag = *Sphagnum magellanicum*; Sph war = *Sphagnum warnstorfii*; Tom nit = *Tomenthypnum nitens*; wood = wood and bark remains.

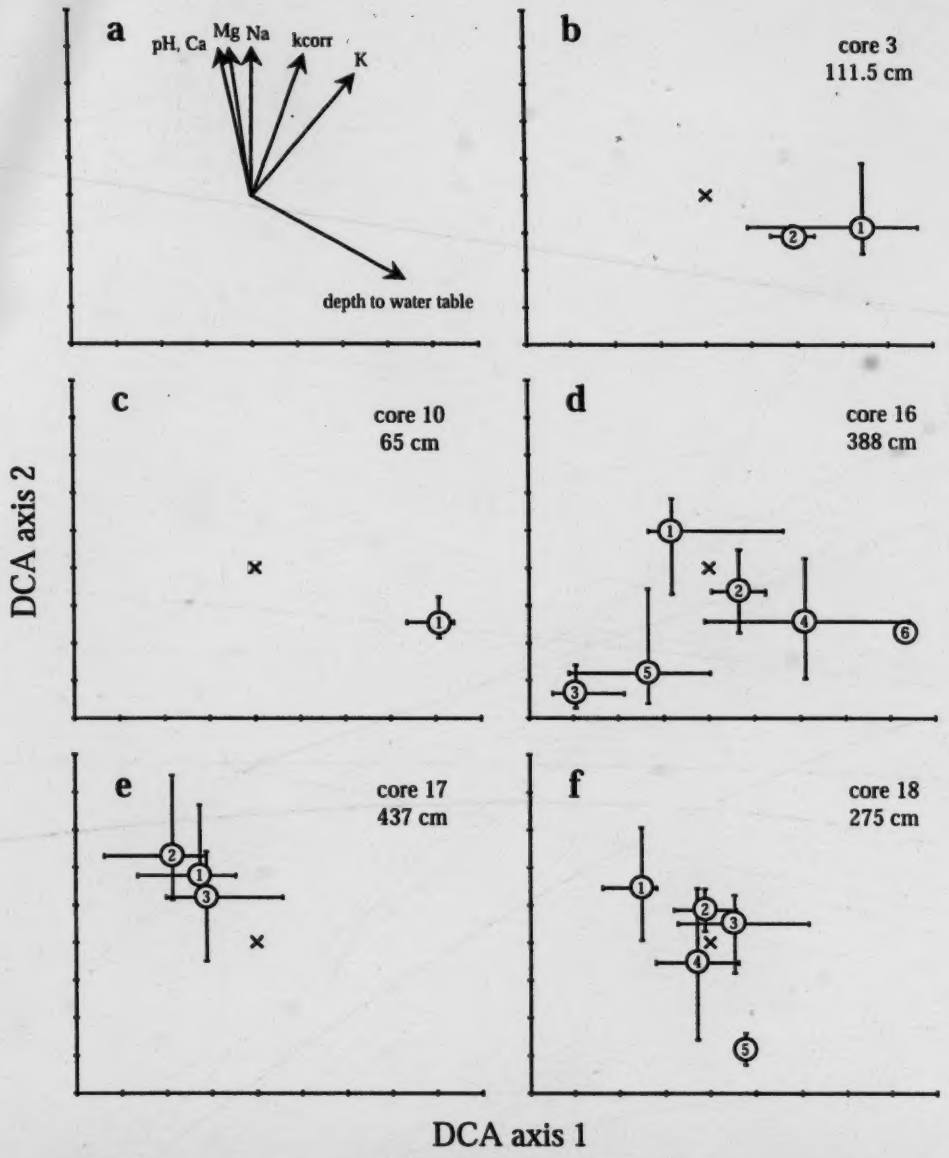


Figure 2.12: (a): Directions of maximum change in environmental variables within the macrofossil ordination (Figure 2.10), based on inferred environmental data for macrofossil samples. All vectors are scaled to the same (arbitrary) length. For further explanation, see text. (b - f): Successional histories of individual cores in ordination space. Each point plotted represents the mean and ranges of DCA axis scores for samples within a stratigraphic zone, as defined by constrained clustering within cores. Zones are numbered from the base upwards. See Appendix 3 for full macrofossil diagrams and position of stratigraphic zones. The cross within each diagram marks the centroid of the ordination plot

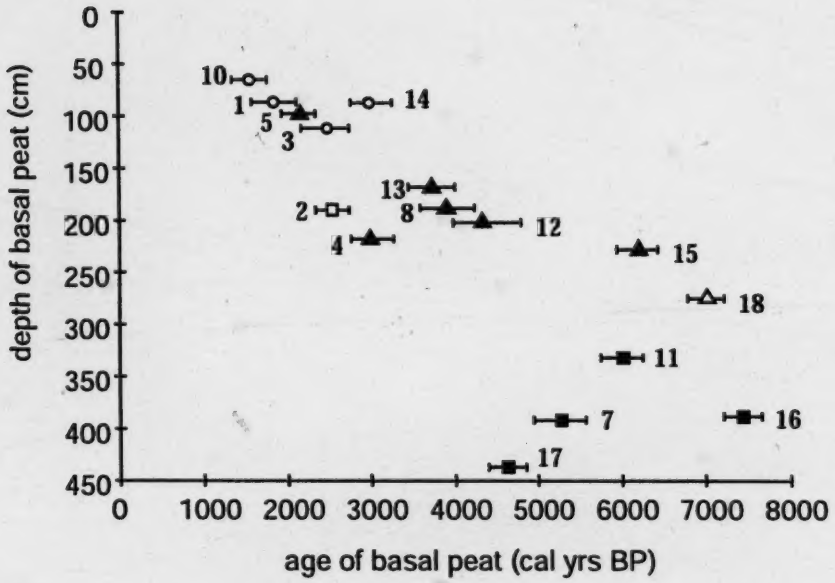


Figure 2.13: Relationship between basal peat age and present peat depth in the study area. Error bars show the calibrated age range of each ^{14}C sample (2σ). Numbers identifying cores are the same as in Figure 2.2. Symbols refer to macrofossil cluster groups. For a list of symbols and characteristic indicator species for each group, see Figure 2.10.

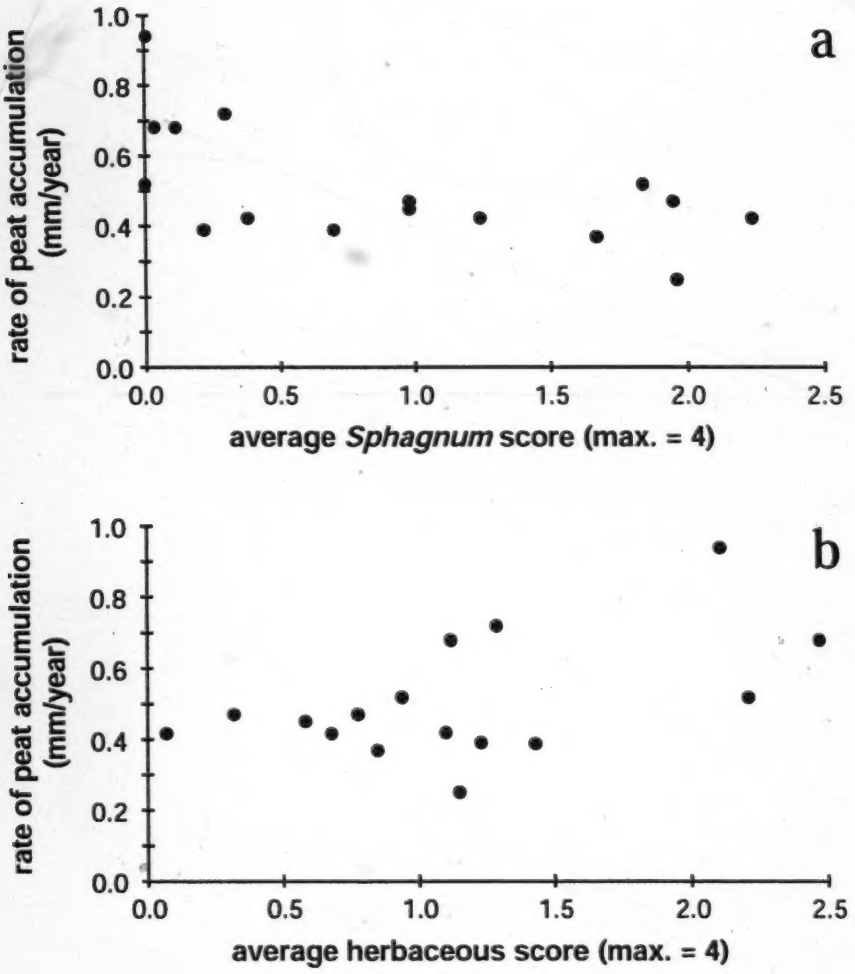


Figure 2.14: Relationship between long-term rates of peat accumulation and the average score for (a) *Sphagnum* (r = -0.58; p = 0.01) and (b) herbaceous material (r = 0.53; p = 0.02) in each core. Peat accumulation rates are corrected for stratigraphic gaps and therefore often lower than those presented in Table 2.2.

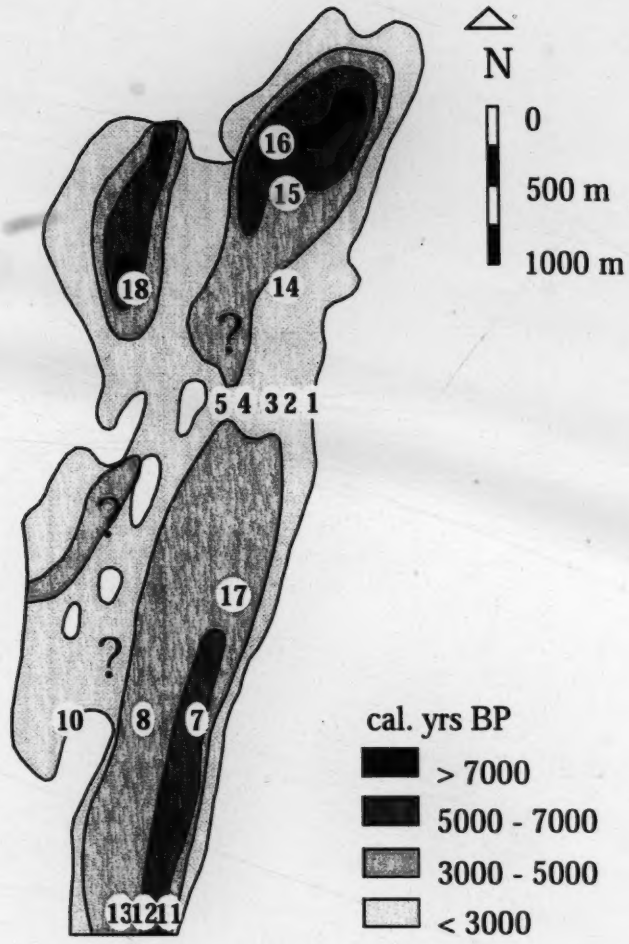


Figure 2.15: Pattern of peat expansion over time, as inferred from basal peat dates. Areas in which present peat depth is less than 40 cm are plotted in white. (Under the Canadian Wetland classification system (Tarnocai *et al.* 1988), only areas of ≥ 40 cm peat depth are classified as peatland). The exact timing of peat initiation in most of the shallow western and north-western regions of the site is unknown.

CHAPTER 3

Peatland development in the discontinuous permafrost zone of northern Alberta

INTRODUCTION

About half of Canada's land surface is underlain by permafrost (Brown 1968; Heginbottom 1995), i.e. ground that remains at or below 0 ℃ for at least two years (French 1996). Climate determines the overall geographic zonation of permafrost, and areas with mean annual temperatures lower than about -8.3 ℃ are underlain by continuous permafrost (Zoltai 1995). Further south in the discontinuous zone, permafrost development is mediated by more localized factors such as physiography and vegetation cover. The southern limit of permafrost distribution roughly corresponds to the 0 ℃ mean annual air temperature isotherm, and close to this limit permafrost occurs only in peatlands (Zoltai 1971). In the boreal and subarctic regions of continental western Canada (Alberta, Saskatchewan and Manitoba), peatlands occupy over 365,000 km^2 of land and store an estimated 48.0 Pg (1 Pg = 10^{15} g) of carbon. Over a quarter of this peatland area (103,000 km^2) is presently underlain by permafrost (Vitt *et al.* 2000).

The thermal properties of peat favour permafrost development because dry peat has low thermal conductivity and insulates the underlying soil during summer. In fall, moisture content increases and higher thermal conductivity of frozen peat allows for effective heat loss (Brown 1968). Perennially frozen ground in peatlands is associated with the development of characteristic landforms. At the southern limit of permafrost distribution, these include treed frost mounds (see Beilman *et al.* 2001 for a discussion of terminology) and internal lawns. Internal lawns are regions of wet, collapsed ground where permafrost used to be present but has melted in response to climatic warming since the Little Ice Age (Thie 1974; Halsey *et al.* 1995; Beilman *et al.* 2001). In regions where mean annual temperatures are below -1 ℃, bogs contain peat plateaus, i.e. regions of perennially frozen ground that are slightly (~1m) elevated over the level of the surrounding land and can extend over several hectares or square kilometers (Zoltai 1971; Vitt *et al.* 1994). In the northern Boreal, mature peat plateaus are covered by black spruce (*Picea mariana*) with a ground cover dominated by lichens and feather mosses (Zoltai 1972).

Peat plateaus often contain collapse scars where permafrost has melted, forming wet thermokarst depressions that are colonized by hydrophytic *Sphagnum* species (mainly *S. riparium* and *S. angustifolium*). Peat accumulation in these depressions leads to rapid vegetation succession and eventual establishment of hummock Sphagna (mainly *S. fuscum*) that provide a dry, insulative surface and allow for permafrost re-aggradation (Zoltai 1993; Camill 1999; Robinson and Moore 2000). Camill (1999) found that succession after thermokarst collapse to hummock communities capable of forming new permafrost could occur within a period of 80 years. Permafrost collapse can be triggered by any factor that disturbs the insulating layer, such as fire (Reid 1977; Zoltai 1993), loss of tree cover (Zoltai 1972; Mackay 1970), and anthropogenic disturbance such as the bulldozing of seismic lines or fire breaks (Mackay 1970; Reid 1977). At the southern limit of permafrost distribution, present climate prevents renewed permafrost development although relict permafrost features may persist (Thie 1974; Halsey *et al.* 1995). Further north, the juxtaposition of different landform types and long-term peat sequences suggest that permafrost collapse and re-aggradation both take place naturally, with collapse-aggradation cycles occurring over periods as short as 600 years (Zoltai 1972; 1993).

Peatlands presently underlain by permafrost mostly initiated in a permafrost-free environment, both in Canada (Zoltai and Tarnocai 1975) and parts of the Russian Arctic (Oksanen *et al.* 2001). Theoretical models based on orbital parameters predict greater seasonality of northern hemisphere climate between 12,000 and 6000 yr BP, with summer insolation up to 8% higher and winter insolation 8% lower than today. This warming trend reached its maximum about 9000 yr BP in western North America, with a delayed response further east because of residual effects of the melting Laurentide ice sheet (Anderson *et al.* 1988; Kutzbach and Webb 1993; Webb *et al.* 1993). The cooling trend that followed this early Holocene insolation maximum followed a similar time-transgressive pattern (Schweger and Hickman 1989; Halsey *et al.* 1998). Major climatic boundaries were displaced northwards during the warm period, and permafrost zones were still shifted by 300 to 500 km compared to their

present position at 6000 yr BP (~ 6800 calendar years before present; cal. yr BP; Zoltai 1995). Vardy *et al.* (1997; 1998) estimate that permafrost initiation occurred about 6300 yr BP (~7000 cal. yr BP) in a peatland on the Tuktoyaktuk peninsula (69.5 °N) and 5000 yr BP (~5700 cal. yr BP) in a peatland near Inuvik (68.3 °N). Zoltai (1993) suggests a minimum date of 3500 yr BP (~3750 cal. yr BP) for permafrost initiation in northwestern Alberta, and data from peatlands in northern Québec (Couillard and Payette 1985) and the Hudson Bay Lowlands (Kuhry 1998) suggest that expansion of permafrost occurred only 2700 and 2200 years ago, respectively.

Little is known about how permafrost initiation affects peatland dynamics at the landscape level. Peatland development is controlled by a mixture of both external (allogenic) and internal (autogenic) factors (e.g. Sjörs 1980; Tallis 1983; Payette 1988; Kuhry *et al.* 1993). Climate, hydrology, physiography and autogenic vegetation succession play interacting roles in controlling both vertical peat accumulation and the lateral expansion of peatlands over time (paludification). The multidimensional nature of this process is hard to capture using traditional means of paleoecological investigation that are essentially one-dimensional (i.e. cores). In order to reconstruct the spatial development of even small peatland sites and understand factors that control local landform differentiation, multiple profiles have to be examined. In permafrost peatlands, this approach has been used by Vardy *et al.* (1997; 1998) in the Northwest Territories, by Couillard and Payette (1985) and Payette (1988) in northern Québec, and by Oksanen *et al.* (2001) in European Russia. All these sites are located either in the Subarctic or Arctic, with mean annual temperatures around -5 °C or less.

This study investigates the development of a peatland complex in the Continental High Boreal wetland region of northwestern Alberta (National Wetlands Working Group 1988). Previous studies in this area (Reid 1977; Zoltai 1993) indicate that peat accumulation began as early as 9000 years BP (~10,200 cal. yr BP) and permafrost first initiated about 4000 years ago (Zoltai 1993). Specific questions examined are: (a) How variable are peat depths and basal peat dates within a site? (b) When were the main periods of lateral peatland expansion, and can these be related to

the paleoclimatic history of the region? (c) How does landform development differ within a site, and what may explain differences in successional pathways?, and (d) How did permafrost initiation affect the overall development of the site?

STUDY AREA

The study site is located at 58°17'N 119°22'W, about 2 km north of the western end of Rainbow Lake and 24 km south of Rainbow Lake townsite (Figure 3.1). The area is part of a northern extension of the Mixedwood section of the Boreal Forest region (Rowe 1972). Climate is cold and continental, with short, warm summers and long, cold winters. Based on climate normals from Fort Nelson (58°50'N 122°35'W) and High Level (58°37'N 117°10'W), mean annual temperature is between -1 and -2 °C, and average annual precipitation about 400 mm. Almost two thirds of this precipitation falls as rain between May and August (Canadian Climate Program 1993).

The bedrock of the region consists of Cretaceous marine shales of the Shaftsbury Formation that are overlain by unconsolidated Quaternary deposits (Borneuf and Pretula 1980). This part of northwestern Alberta was deglaciated about 12,000 yr BP (14,000 cal. yr BP; Dyke and Prest 1987), and most of it is covered by dead-ice moraine of low to medium relief, sometimes topped by lacustrine deposits (Bayrock 1960). The area immediately surrounding the study site is underlain by till, with textures ranging from sandy clay loam to silty clay (Lindsay *et al.* 1960). Topography is level to undulating, with slopes of 0-1.5 percent (Lindsay *et al.* 1960). The southern edge of the study site occupies an elevation of about 503 m above sea level, and from there the terrain slopes gently (<1%) north- and north-westwards, towards an unnamed tributary of the Hay river. There is no evidence for well-developed drainage channels, and at least the southern part of the site may drain directly southwards into the Hay River.

The region is part of the Sporadic Discontinuous Permafrost zone where 10-50% of the land area is underlain by permafrost (Heginbottom 1995). In peatlands, peat plateaus are the dominant permafrost-related landform class (Beilman *et al.* 2001). In the study site, peat plateaus constitute about 40% of the peatland area while the remaining 60% are made up of fen communities. Fens are mostly dominated by *Carex* sp. (*C. lasiocarpa* and *C. aquatilis*), often with a dense cover of *Salix* sp. or *Betula pumila*. Stunted *Larix laricina* are present in many areas, and *Alnus* is abundant on shallow peat. Bryophyte cover is variably developed and, where present, includes species such as *Hamatocaulis vernicosus, Calliergon* sp., *Amblystegium* sp, *Sphagnum warnstorfii* and *Tomenthypnum nitens*. *Potentilla palustris* and *Cicuta* sp. grow in wetter areas. Some of the regions referred to as fens here resemble deciduous swamps *sensu* Vitt *et al.* (1996), i.e. they have a dense cover of *Salix* spp that grow above shoulder height and a poorly developed bryophyte cover.

With few exceptions, peat plateau areas contained no permafrost at the time of sampling. The site was burned in a lightening-induced wildfire that covered over 4500 acres (~18.2 km^2) in the summer of 1971 (Fire # DF3-029-71). Presumably as a result of this fire and intensive seismic exploration, permafrost has degraded throughout the peat plateau areas. In the southwestern part of the site, the burn margin corresponds to the study area boundary and separates intact peat plateaus from areas where permafrost has collapsed. Intact peat plateaus are covered by tall *Picea mariana* with a ground layer dominated by feather mosses and *Sphagnum*. Collapsed plateau areas resemble dry continental bogs and are dominated by *Sphagnum fuscum*, often mixed with *Polytrichum strictum* and lichens. Common vascular taxa include *Ledum groenlandicum, Rubus chamaemorus, Vaccinium vitis-idea* and *Chamaedaphne calyculata*. *Sphagnum angustifolium* and *S. riparium* are abundant in wetter areas. Some of these may not have contained permafrost prior to the fire, i.e., represent areas that used to be collapse scars *sensu* Vitt *et al.* (1994). *Picea mariana* are regenerating throughout the collapsed plateau area (Figure 3.2).

METHODS

Field sampling

A 6.5 km^2 study area was selected for this investigation (Figure 3.3). Peat landforms (fen and collapsed peat plateau) are bounded by upland or treed swamp along most of its perimeter. The site was surveyed in July 1996 and August 1998. Peat depth was measured to the nearest 10 cm at 25 or 50 m intervals along a series of transects (Figure 3.3). Wherever possible, the nature of the underlying mineral material was noted. In 1996, many areas of the peatland still contained seasonal frost. Survey points where this layer could not be penetrated were discarded, yielding a total of 265 depth measurements to mineral. Eleven coring sites were selected from the survey points (Figure 3.3). Five of these (nos. 5, 6, 7, 8 and 10) represent dry continental bog in collapsed peat plateau areas. Core 3 is from a wet depression surrounded by relict peat plateau. Four sites (nos. 1, 2, 4 and 11) represent fen communities, mostly close to marginal swamp or upland. The environment at coresite 9 is intermediate between peat- and upland. The term 'swamp' is used here because it describes a forested non peat-accumulating wetland, usually with marked seasonal water table fluctuations. Organic matter accumulation at the site is just over 40 cm, but the local vegetation includes taxa characteristic of both peat- and upland habitats (e.g. *Salix* sp., *Picea mariana*, some *Betula papyrifera*, *Calamagrostis canadensis*, *Equisetum arvense*, *Achillea millefolia*, *Parnassia palustris*, *Tomenthypnum nitens* and *Aulacomnium palustre*).

Cores were taken using a modified Macaulay peat sampler or by sampling the side of a shallow pit if peat depth was insufficient for coring. Duplicate cores were taken at some shallow sites (nos. 4, 5, 6 and 7). Cores were stored in half-sections of PVC pipe wrapped in plastic film.

Core sampling and description

In the laboratory, samples of known volume (2.5 - 5.0 cm^3) were taken at 10 cm intervals along cores, air-dried for 48 hours, ground to a fine powder and combusted for four hours at 550 ℃ to measure loss on ignition (organic matter content). 'Basal peat' is here defined as the deepest section of each core that has an organic matter content of ≥80% (see Chapter 2 for further discussion). A bulk peat sample (usually 4 cm in length) was removed from the base of each core, dried at 80 ℃ for 24 hours and submitted to either the Geological Survey of Canada (GSC) or the radiocarbon laboratory of Brock University (BGS) for ^{14}C age determination. All dates were calibrated in CALIB rev.4.1 (Stuiver and Reimer 1993) using the INTCAL98 dataset (Stuiver *et al.* 1998) and method B (probability distribution). Calibration curves were smoothed by the calendar year span contained within each ^{14}C sample, assuming that one centimeter of peat represents 50 years of accumulation. This number is close to the average long-term accumulation rate for the 11 cores. All dates reported are in calendar years before present (cal yr BP). Long-term apparent rates of peat accumulation were calculated for all cores from the depth and ^{14}C age of basal peat samples. Accumulation rates do not incorporate bulk density and are therefore rates of *height* rather than mass accumulation (see Chapter 2).

Macrofossil samples (2.5-5 cm^3; n = 173) were removed at 10 cm intervals from all cores. Subsamples were distributed evenly on a channeled Plexiglas template, and percent frequencies were estimated for all bryophyte taxa, selected categories of vascular plant remains, lichen fragments, and charcoal. Reference material used in macrofossil determination and concepts used for important bryophyte taxa are listed in Appendix 2. Nomenclature follows Moss (1983) for vascular plants, Anderson (1990) for *Sphagnum* and Anderson *et al.* (1990) for all other mosses. For lithological description, each sample was assigned to one of five peat types (*Sphagnum* peat, woody *Sphagnum* peat, moss/herbaceous peat, woody moss/herbaceous peat or woody peat). Bryophyte taxa generally associated with S*phagnum*-dominated habitats (*Pohlia*

nutans / P. sphagnicola, Mylia anomala and *Polytrichum strictum*) were counted as *Sphagnum*. Otherwise, the classification used was the same as in Chapter 2 (Figure 2.6).

Analysis of macrofossil data

Clustering and ordination

Cores were divided into zones by stratigraphically constrained minimum variance clustering of macrofossil data (Ward 1963; Birks and Gordon 1985). The aim of clustering was not to describe individual profiles in detail, but rather to identify major stratigraphic transitions and compare developmental patterns between cores. The variance cutoff was chosen accordingly (1.0 Squared Euclidean distance). At this cutoff, there were no interpretation problems associated with reversals (i.e. instances where the joining of two adjacent clusters leads to a *decrease* in within-cluster dispersion).

After removal of rare species (taxa with fewer than three occurrences), all macrofossil samples from ≥ 10 cm depth (n = 162) were subjected to a combined cluster analysis, again using Ward's minimum variance method (Ward 1963). Surface samples were excluded because they often differed in botanical composition from the peat below and contained a disproportionate number of rare species. Indicator species for cluster groups were identified following the method of Dufrêne and Legendre (1997; see Chapter 2). The 162 samples were subjected to ordination by non-metric multidimensional scaling (NMDS; e.g. Clarke 1993), with Relative Euclidean distance as distance measure. Multiple preliminary runs from random starting configurations were performed with both the original and randomized data in order to determine the dimensionality most appropriate for the dataset. Dimensionality is considered optimal if addition of a further axis decreases stress by less than five (on a scale from 0-100), and stress at this dimensionality is significantly lower than in runs using randomized data (see McCune and Mefford 1999 for further explanation). Based on these criteria, a three-dimensional solution was selected, and the best three-dimensional

configuration obtained during preliminary runs was used as starting configuration for the final ordination.

Charcoal content

In order to examine the relationship between macrofossil composition and charcoal content (CHARCOAL: presence / absence of ≥ 2% charcoal) of samples, macrofossil data were summarized into seven functional groups: *Sphagnum* Sect. Acutifolia (SPHA); *Sphagnum* Sect. Cuspidata (SPHC); bryophytes usually associated with *Sphagnum* (BBRYO; see above); other bryophytes (OBRYO); remains of woody plants (WOODY); herbaceous remains (HERB); and lichens (LICHEN). WOODY was log transformed in order to linerarize its relationship to the logit of CHARCOAL. LICHEN, BBRYO and OBRYO were coded as binary variables because they were absent from most samples. Sample depth and functional group variables were used in a stepwise forward selection logistic regression analysis. A separate analysis was run using sample scores from the NMDS axes (NMDS1, NMDS2 and NMDS3) as predictors.

Peat depth distribution

Field measurements of peat depth (probe depth) significantly overestimated basal depth (20% ash limit) at core locations, with an average difference of 37 cm between the two measurements (paired *t*-test, $t = 3.268$, $p<0.01$). Probe depths were converted to basal depth values using Model II (Major Axis) regression (Figure 3.4). Model II regression is the appropriate method for determining the functional relationship between two variables that are both measured with error (Sokal and Rohlf 1995; Legendre and Legendre 1998). For forecasting (i.e. prediction of one variable from the other) many authors (Sokal and Rohlf 1995; Legendre and Legendre 1998) recommend use of ordinary least squares (OLS) techniques even in Model II situations, while others suggest that use of the functional relation is appropriate in many cases (see Ricker 1973 for a detailed review). For this particular dataset, examination of residuals indicated that the Major Axis provided a better fit than OLS

when probe depth was ≤150 cm, which is the case for 80% of measured probe depth values.

Because the limited number and spatial distribution of depth measurements did not allow for effective interpolation, five hundred realizations of peat depth throughout the site were generated from the calibrated probe values by sequential indicator simulation (Isaaks 1990; Goovaerts 1997). Unlike spatial interpolation techniques such as kriging, stochastic simulation is not aimed at providing a unique 'best' estimate at each location of interest. Rather, a Monte Carlo approach is used to generate a set of equiprobable realizations that reproduce the statistical properties of the process under study, including the sample (or other specified) cumulative distribution function (*cdf*) and the spatial covariance structure of the input sample (see e.g. Deutsch and Journel 1998; Goovaerts 1999).

In sequential indicator simulation, a prediction is generated at each grid node by randomly drawing from the local probability distribution, built by kriging at a series of cumulative indicator thresholds. Simulated nodes are used as input values when generating subsequent nodes, i.e. successive nodes are generated with increasing conditioning (see Goovaerts 1997 for a good description of the method and underlying theory). Unlike parametric (Gaussian) algorithms, indicator simulation does not make any *a priori* assumptions about the shape of local probability distributions. Because a separate variogram model is fitted at each indicator threshold, changes in covariance structure between thresholds (e.g., greater spatial continuity of high data values) can be incorporated into the simulation. The indicator approach is also flexible in allowing for incorporation of soft prior probabilities derived from auxiliary information. In this study, preliminary analysis showed systematic differences in peat depth between landforms (Kruskal Wallis non-parametric ANOVA; $H_c = 81.65$, $p < 0.001$; Figure 3.5), and prior probabilities were assigned to each grid node based on mapped landform type (Figure 3.3).

Indicator variograms were modelled at depth thresholds roughly corresponding to the nine deciles and 95th percentile of the input sample. Because probe depth had

only been measured to the nearest 10 cm, the calibrated input sample *cdf* contained discrete stepwise increases at basal depth values corresponding to 10 cm intervals in the original probe data. All indicator cutoffs were placed at the midpoint between such steps. An omnidirectional exponential model with nugget effect was fitted to the data at each indicator threshold by iteratively reweighted least squares (Figure 3.6). All variograms were fitted over a range of 1600 meters. Simulation was done using a modified version of program sisim_lm in GSLIB (Deutsch and Journel 1998) that allowed specification of the study area boundary as a mask map. The target global (marginal) *cdf* was an average of the prior distributions for different landform types, weighted by the area occupied by each landform within the study area.

RESULTS

Peat depth distribution

Changes in variogram parameters between successive indicator thresholds (Figure 3.6) indicate that spatial covariance changes with depth. Variograms for the first five indicator thresholds (0-84 cm) have relative nugget effects between 25 and 40%, indicating uncertainty at short separation distances followed by a gradual increase in semivariance as distance increases further. Effective range decreases with peat depth, indicating that upland and shallow peat areas are spatially continuous over large distances, whereas high (deep) depth values occur in small, spatially isolated clusters. The dip in semivariance ('hole effect') observed at the last three indicator thresholds at 800-1200 meters (Figure 3.6) suggests that these areas of deep peat are spaced 800-1200 meters apart.

The mean prediction for each grid node from the 500 simulations (Figure 3.7a) shows two distinct peat basins: a small, deep area in the south, and a larger region of variable peat depth that occupies most of the northern half of the site. Figures 3.7b-f show five realizations from stochastic simulation. Differences between realizations reflect the degree of uncertainty associated with each grid node. Nodes for which basal depth can be predicted with relative certainty show similar simulated values across all

realizations, whereas marked differences between realizations reflect a high degree of local uncertainty. Overall, simulation results support the notion of two peat basins, although these are connected in several realizations. Low simulated values are concentrated in areas classified as upland or swamp, and patches of deep peat occur under peat plateau regions, reflecting use of prior landform-based probabilities. Except close to actual measurements, the location of deep areas varies markedly between realizations, i.e., their position cannot be predicted with certainty given the data available.

Macrofossil stratigraphies

Fen and swamp cores

Constrained clustering failed to subdivide the profiles of cores 1 and 4 (Figures 3.8a and b), indicating that little community change has occurred at these points over time. Basal deposits of both cores consist of a mixture of herbaceous and wood or bark remains. In core 4 (30 cm total depth; Figure 3.8b) no new taxa appear except for some smooth woody roots in the surface sample. There is a charcoal layer at 20 cm depth, and herbaceous remains increase in abundance towards the top of the profile. Core 1 (120 cm total depth; Figure 3.8a) contains layer of *Calliergon giganteum* mixed with dicot leaves between 80 and 110 cm. A layer of woody peat with charcoal at 70 cm depth is overlain by 30 cm of herbaceous peat, with more charcoal at 40 and 50 cm. *Hamatocaulis vernicosus* and *Larix* needles increase in abundance above 20 cm depth. The coring site is presently a shrubby rich fen, and the needles may originate from a tall stand of *Larix* located about 30 m farther east.

Coresite 11 represents a small, wet flow channel at the transition between herbaceous fen and treed swamp. The core is 160 cm long, and basal deposits consist of wood and bark remains mixed with charcoal (Figure 3.8d). Between 20 and 160 cm (zone 11.1) the peat is predominantly herbaceous, with varying proportions of woody plant remains. Bryophytes are absent, except for isolated leaves of *Sphagnum warnstorfii* and *Hamatocaulis vernicosus*. *Larix* needles and dicot leaves are present

intermittently from about 150 cm onwards, and *Picea* needles and ericaceous roots appear at 60 and 30 cm depth, respectively. The beginning of zone 11.2 (0-10 cm), which is dominated by *Polytrichum strictum* and *Pohlia*, is marked by a distinct charcoal horizon.

Peat from core 9 (marginal swamp; Figure 3.8c) is dominated by woody plant remains between 10 and 40 cm depth, including wood and bark fragments, roots, and dicot leaves. This core contains several woody root types not found in other cores. Charcoal and conifer needles occur sporadically at frequencies below 1%. The surface sample is dominated by *Tomenthypnum nitens.*

Core 2 (Figure 3.9) is the deepest of the fen cores and contains three stratigraphic zones. Zone 2.1 (170-190 cm) is dominated by herbaceous and wood / bark fragments, with occasional woody roots and *Larix* needles. The basal sample contains almost 20% charcoal. Zone 2.2 (140-160 cm) is dominated by *Sphagnum warnstorfii. Larix* needle fragments and robust woody roots are present throughout, and ericaceous remains appear at 150 cm depth. The basal sample of zone 2.3 (0-130 cm) contains *Warnstorfia exannulata* and *Hamatocaulis vernicosus.* Herbaceous remains, woody roots and dicot leaves are present at 110-120 cm, and the upper 100 cm of the profile consist of *Sphagnum* peat, with *S. angustifolium* and *S. fuscum / S. capillifolium* alternating in dominance. *S. riparium* is abundant at 20 cm depth. Several stratigraphic gaps are evident in the upper part of the core. The coresite is a wet depression surrounded by treed poor fen, and low bulk density of the surface peat caused slumping and perhaps loss of material during coring.

Peat plateau cores

Deep cores

The deepest core taken in this study (Core 8; Figure 3.10) comes from an area of collapsed peat plateau in the northeastern part of the site. The basal section (zone 8.1; 250-330 cm) is dominated by herbaceous remains, and samples from 300-330 cm contain between 40 and 65 percent *Sphagnum* in a mixture of *S. fuscum / S.*

capillifolium and *S. angustifolium*. Woody and other bryophyte remains are rare. Seeds of *Typha*, *Menyanthes* and *Eleocharis* were recovered from this zone, and most samples contained cladoceran egg cases.

The basal sample of zone 8.2 (70-240 cm) contains remains of *S. warnstorfii*, *Aulacomnium palustre* and *Hypnum pratense* and marks an abrupt transition between herbaceous peat below and *Sphagnum* peat above. *S. fuscum / capillifolium*, *S. angustifolium* and *S. riparium* replace each other throughout zone 8.2, and ericaceous remains are present throughout. Dicot leaves, robust woody roots and wood / bark fragments appear intermittently, and samples from 220 and 180 cm contain abundant robust woody roots. Zone 8.3 (0-60 cm) initially resembles zone 8.2, with high abundances of *S. angustifolium* and *S. riparium*. At 40 cm, there is a layer of charcoal mixed with *Polytrichum* remains. This is followed by a gap in the stratigraphy and herbaceous peat that is gradually replaced by ericaceous remains in the uppermost samples

The stratigraphy of core 10 (Figure 3.11) is initially similar to that of core 8. Zone 10.1 (220-300 cm) is dominated by herbaceous remains, with *S. fuscum / capillifolium* and *S. angustifolium* in the basal sample. *Eleocharis* and *Typha* seeds occur in several samples, and bryophytes (*Aulacomnium palustre*, *Bryum pseudotriquetrum*, *Campylium stellatum* and *Tomenthypnum nitens*) first appear at 250 cm depth. Zone 10.2 (200-210 cm) is dominated by *Tomenthypnum nitens*, with some *Bryum pseudotriquetrum* and isolated leaves of *Aulacomnium palustre* and *Calliergon giganteum*. Dicot leaves and conifer needles (both *Picea* and *Larix*) are present in the upper sample.

Zone 10.3 (120-190 cm) initially contains a mixture of Sphagna (*S. fuscum / S. capillifolium* and *S. angustifolium*) and brown mosses such as *Tomenthypnum nitens* and *Calliergon giganteum*. Both *Picea* and *Larix* needles are present, and dicot leaves occur at relatively high frequencies. The upper half of zone 10.3 is dominated by wood / bark fragments and woody roots, with *Larix* needles and dicot leaves at 150 cm. The final zone (10.4; 0-110 cm) is dominated by *S. fuscum / capillifolium*, with *S. riparium*

and *S. angustifolium* between 80 and 50 cm depth. The sample at 10 cm depth consists of lichen remains mixed with charcoal and woody roots. The surface sample contains *S. fuscum / capillifolium* mixed with *Mylia anomala, Pohlia* sp. */ Polytrichum strictum* and ericaceous remains.

Core 3 (Figure 3.12) is the only core that was taken in an environment still surrounded by intact permafrost. Zone 3.1 (190-250 cm) is initially made up of herbaceous remains with wood and bark fragments; dicot leaves, *Larix* and *Picea* needles, and *Tomenthypnum nitens* appear towards the top of this zone. Zone 3.2 (90 - 180 cm) is dominated by *S. fuscum / capillifolium.*, and no other *Sphagnum* species were found. Ericaceous remains and *Picea* needles are present throughout this zone, and *Larix* needles in the lower half. The final zone (3.3; 0-80 cm) begins with a sample dominated by *S. angustifolium* and *S. riparium* mixed with charcoal. The following samples show a succession first to *S. fuscum / capillifolium* and then to predominantly woody remains and robust woody roots. *Picea* needles are abundant at 10 - 20 cm depth. The core was taken in a wet pool, and the surface sample is dominated by *Calliergon giganteum* and *Plagiomnium ellipticum.*

Shallow cores

The three shallow peat plateau cores (nos. 5, 6 and 7; Figure 3.13a-c) were all taken close to the margin of plateau areas in the southern half of the site. All three are dominated by *Sphagnum fuscum / S. capillifolium* for most of their development, and constrained clustering did not produce separate zones except in the case of core 5 (Figure 3.13a) where there is an abrupt shift to *S. angustifolium* in the basal sample. The basal samples of core 6 consist of woody and herbaceous remains mixed with charcoal, and those of core 7 contain a mixture of *S. fuscum / S. capillifolium* and robust woody roots. All three cores contain distinct layers of lichen and woody remains mixed with charcoal. In cores 5 and 6, these are close to the base, and in core 7 they appear at 50 cm depth. The three cores contain varying proportions of woody fragments and robust woody roots, and ericaceous remains become increasingly

abundant towards the surface. Surficial samples contain *S. fuscum / S. capillifolium* mixed with *Mylia anomala, Pohlia* sp. or *Polytrichum strictum.*

Clustering and ordination

Clustering of the combined macrofossil data was terminated at the eight cluster level. The eight groups and their indicator taxa are summarized in Table 3.1.

Cluster group 3 is characterized by high frequencies of herbaceous remains. Herbaceous remains are ubiquitous in the dataset and reach their highest indicator value (85.2) at cluster level 2. Their association with cluster group 3 reflects the fact that samples from this group generally contain few other remains. Smooth woody roots are the only significant indicator taxon for cluster group 1, with a relatively low indicator value (17.0). Non-ericaceous dicot leaves and *Calliergon giganteum* reach high relative abundances in this cluster, and herbaceous remains occur in every sample. Significant indicator taxa for cluster group 2 are wood / bark remains and miscellaneous roots. Herbaceous remains are present in every sample and reach their third highest relative abundance in this cluster.

Cluster group 7 has three indicator species: robust woody roots, *Sphagnum warnstorfii,* and *P. mariana* needles. The remaining four clusters are largely defined by bryophyte indicator species. Clusters 6 and 4 are associated with *S. fuscum / S. capillifolium* and *S. angustifolium,* respectively. *Sphagnum riparium* is a significant indicator species for cluster 5. However, its indicator value (21.5) is low because it is not a reliable indicator for the group, i.e. it is absent from many of the samples. *Polytrichum strictum* is the only significant indicator taxon for cluster 8, with the highest indicator value observed in this study (90.1).

The NMDS ordination for the macrofossil data is shown in Figure 3.14. Final stress for the three-dimensional solution was 11.33, indicating that relative similarities between samples are summarized well by their distances in ordination space. While most cluster groups separate well, overlap is considerable in some cases. Group 7 (robust woody roots / *Sphagnum warnstorfii* / *Picea mariana*) is poorly defined on

axis 2, and Group 8 (*Polytrichum strictum*) scores widely overlap those of adjacent clusters on all three axes.

Distribution of charcoal

The distribution of charcoal with depth in the 11 cores (Figure 3.15) shows several peaks. Charcoal was never recovered from all samples of a given depth, and increased recovery of charcoal from the top 100 cm may partially reflect the greater number of samples available for this depth interval. NMDS axis scores were not significant predictors of CHARCOAL (presence / absence of ≥2% charcoal in a sample) in univariate analysis (Table 3.2). Of the functional macrofossil categories examined, WOODY and LICHEN produced significant results, both with positive slopes indicating increased probability of recovering charcoal from samples containing these types of remains. There was a significant negative relationship between CHARCOAL and depth, suggesting that the pattern apparent in Figure 3.16 is not a sampling artifact. Stepwise forward selection identified WOODY and LICHEN as the most important predictor variables (Table 3.3). Once they are taken into account, inclusion of depth does not explain a significant ($\alpha = 0.05$) amount of additional deviance ($G = 3.22$; $p = 0.073$). The two-variable model is highly significant ($G_M = 19.991$, $p < 0.0001$) but explains only 12.3% of the total deviance.

Basal peat dates an rates of peat accumulation

Basal peat dates span 8000 years, ranging from 10,230 to 2120 cal. yr BP (Table 3.4). The three oldest dates come from the deep peat plateau cores (nos. 8, 10 and 3), and the youngest from the marginal swamp area (no. 9). There is a strong positive relationship between basal age and peat depth (Spearman $r_s = 0.91$; $p<0.01$). Fitting of linear and exponential models results in R^2 values of 0.83 and 0.85, respectively (Figure 3.16a). The linear model intersects the X-axis at 2340 cal. yr BP, predicting non-recent ages for surface peat.

Long-term rates of apparent peat accumulation range from 0.07 to 0.32 mm/year. (Table 3.4; Figure 3.16b). There is a weak but significant positive correlation between the rate of peat accumulation and basal peat age (r=0.62; p<0.05). Exclusion of core 9 from the marginal swamp area increases the strength of this relationship (r=0.76; p<0.01). Mean rates of long-term peat accumulation are similar among the three deep plateau cores (mean = 0.32 mm/yr.; range 0.31-0.33) and twice as high as those of the shallow plateau cores (mean = 0.16 mm/yr.; range 0.14-0.17). The four fen cores differ widely in long-term accumulation rates (mean = 0.23 mm/yr.; range 0.07-0.30), with a general trend of slower rates in cores that initiated more recently (Figure 3.16b).

INTERPRETATION

Patterns of community development

The mixture of woody and herbaceous remains at the base of the four fen cores (nos 1, 2, 4, and 11) is similar to the macrofossil composition of core 9 (marginal swamp), indicating that these areas originated by swamping (paludification) of upland forest. Initial peatland communities at all four sites were monocot-dominated shrubby fens. At coresite 2 this phase was brief, and a treed fen with *Larix laricina* and ericaceous shrubs became established (Zone 2.2; Figure 3.9). *Sphagnum warnstorfii*, which is abundant in this zone, is a characteristic hummock species in moderate-rich fens (Gignac and Vitt 1990). *Calliergon giganteum* and *Hamatocaulis vernicosus*, both recovered from core 1, are also indicative of moderate-rich fen environments but generally occupy wetter microsites than *S. warnstorfii* (Chee and Vitt 1989, Nicholson and Gignac 1995).

In cores 1 and 11, *Larix* needles increase in abundance towards the surface, suggesting decreasing water tables and invasion by trees. Taxa present in the upper 10 cm of core 11 (*Polytrichum strictum* and *Pohlia*) are characteristic colonizers of burnt peat (Lewis *et al.* 1928; Kuhry 1994). In spite of this apparent drying trend, Cores 1, 4, and 11 remained moderate-rich fens throughout their development. At coresite 2,

Sphagnum fuscum / S. capillifolium, *S. angustifolium*, and *S. riparium* alternate in dominance in the upper 100 cm of peat. *Sphagnum fuscum* and *S. angustifolium* are widespread species characteristic of poor fens or bogs, and the presence of *S. riparium* suggests wet, weakly minerotrophic areas such as permafrost collapse scars (Nicholson and Gignac 1995). The successive replacement of these species is reminiscent of patterns occurring during cycles of permafrost collapse and re-aggradation (Zoltai 1993), although it is unclear if permafrost was ever present at this site.

The basal zones of the three deep peat plateau cores (nos 3, 8 and 10; Figures 3.12, 3.10 and 3.11, respectively) are dominated by herbaceous remains and represent wet fen or marsh environments. At coresite 3, this initial fen was shrubby, whereas the paucity of woody remains in cores 8 and 10 indicates relatively open conditions. The presence of *Sphagnum* at the base of the latter two cores is surprising. In core 8, organic matter content falls below 80% between 305 and 315 cm depth, suggesting that peat accumulation at this site began under wet conditions, perhaps in a shallow pool with a floating *Sphagnum* mat. Alternatively, paludification may have begun under relatively dry conditions, followed by flooding with geogenous water. In either case, seeds of *Typha*, *Menyanthes* and *Eleocharis* and cladoceran egg cases suggest that marshes or shallow ponds with emergent vegetation became established at coresites 8 and 10 during the early Holocene (Shay and Shay 1986; Hann 1990).

In all three deep peat plateau cores, the initially herbaceous communities become invaded by bryophytes. This is most marked in core 10, and taxa recovered, such as *Campylium stellatum*, *Bryum pseudotriquetrum* and *Tomenthypnum nitens*, are indicative of rich fen conditions (Chee and Vitt 1989; Nicholson and Gignac 1995). This is followed by generally abrupt transition to *Sphagnum*, and the upper zones of the three cores are dominated by Sphagna and woody remains. In core 8, cyclic replacement of *S. fuscum / S. capillifolium*, *S. riparium*, and *S. angustifolium* suggests repeated permafrost collapse and re-aggradation (Zoltai 1993). The sample from 220 cm depth contains woody roots mixed with *Picea* needles and most likely represents sylvic peat deposited on a peat plateau. Permafrost-related patterns of community

succession are less apparent in the other two cores. Core 10 shows one potential collapse / re-aggradation sequence between 70 and 40 cm depth, and the upper section of core 3 (10 - 50 cm depth), as well as a lichen-rich layer at the top of core 10, most likely represent peat plateaus.

The shallow peat plateau cores (nos 5, 6 and 7) originated by paludification of upland forest. All are *Sphagnum*-dominated throughout and contain distinct layers of lichen and woody remains mixed with charcoal that are indicative of dry forest microenvironments or peat plateaus. *Sphagnum riparium* was not recovered from any of these cores. The presence of *Mylia anomala, Pohlia* sp. or *Polytrichum strictum* in surface samples is most likely attributable to the 1971 fire.

Clustering and ordination

Cluster group 3 (herbaceous remains) represents emergent marsh and open monocot fens. Other clusters with high abundance of herbaceous remains are number 1 (smooth woody roots) and 2 (wood / bark remains, miscellaneous roots). Significant indicator taxa for these clusters have broad taxonomic affinities and do not allow for assignment to distinct community types. Cluster 1 (smooth woody roots) shows high relative abundances of non-ericaceous dicot leaves (mostly *Salix* and *Betula*) and several samples contain *Calliergon giganteum*, a characteristic species of moderate-rich fens (Chee and Vitt 1989). Based on the presence of these taxa, cluster 1 is tentatively classified as shrubby moderate-rich fen. Cluster 2 (wood / bark remains, miscellaneous roots) most likely represent a variety of community types including swamp, paludifying forest, and permafrost peat plateau.

Samples from Cluster group 7 (robust woody roots, *Sphagnum warnstorfii*, and *Picea mariana* needles) again represent several community types, including dry, woody fen or bog microhabitats and permafrost peat plateaus. Clusters 6 (*S. fuscum* / *S. capillifolium*) and 4 (*S. angustifolium*) correspond to hummock and hollow habitats in bogs or poor fens. *Sphagnum riparium* (Cluster 5) is characteristic of wet, weakly minerotrophic areas such as permafrost collapse scars (Nicholson and Gignac 1995).

However, *S. riparium* is absent from many samples in this group, and mixtures of *S. fuscum / capillifolium* and *S. angustifolium* are common. Cluster 8 (*Polytrichum strictum*) represents recently burnt areas that may be quite variable in base status. *P. strictum* is characteristically associated with dry *Sphagnum* hummocks (Crum and Anderson 1981), but is also a rapid colonizer of disturbed areas such as cutlines and burnt peat where it can reach high cover values (Lewis *et al.* 1928; Kuhry 1994). The same is true for *Pohlia nutans / P. sphagnicola* and *Mylia anomala,* which are not significant indicator species but peak in relative abundance in this cluster.

The lack of clear ecological affinities of some macrofossil cluster groups is mirrored in the ordination results. Cluster 8 in particular overlaps widely with other groups, presumably because it represents a community that develops in response to disturbance and is not constrained by environmental gradients such as water table and pH that normally determine community composition in peatlands. Axis 1 separates bryophyte-dominated clusters (groups 4, 5 6 and 8) from groups dominated by vascular taxa (nos. 1, 2 and 3). Bog and poor fen communities (groups 4, 5 and 6) are mostly well-defined. The position of group 5 (*S. riparium*) between groups 4 (*S. angustifolium*) and 6 (*S. fuscum*) reflects the fact that most group 5 samples contain a mixture of *S. fuscum* and *S. angustifolium*. Points from groups 1 and 3 (herbaceous and shrubby fen) overlap on the ordination diagram because both groups are rich in herbaceous remains. The position of cluster groups 2 and 7, which have very broad ecological affinities in spite of their apparently similar macrofossil composition, complicates ecological interpretation of the ordination.

DISCUSSION

Development of the Rainbow Lake site

Before 8000 cal. yr BP

The timing of peatland initiation at the Rainbow Lake site fits well into what is known about the paleoecological history of the region. Vegetation cover immediately

following deglaciation was probably sparse and included *Betula glandulosa, Populus, Salix, Juniperus,* herbs and graminoids (Vance 1986; MacDonald 1987a;b). This type of community lacks modern analogues in northwestern North America and has been variously interpreted as tundra, parkland, or grassland (see Vance 1986). Between 10,000 and 8500 yr BP (11,400-9500 cal. yr BP), spruce forest started to dominate the Mackenzie Basin (MacDonald 1987b). According to Vance (1986), *Picea* first arrived at around 11,000 yr BP (13,000 cal. yr BP) at Eaglenest Lake (57 °46'N, 112 °06'W; Figure 3.1), and MacDonald (1987a) placed its arrival at about 10,000 yr BP (~11,400 cal. yr BP) at Lone Fox (56 °43'N, 119 °43'W), Yesterday (56 °46'N, 119 °29'W) and Snowshoe (57 °27'N, 120 °40'W) Lakes. Further north at Lac Ciel Blanc (59 °31'N, 120 °11'W) and Wild Spear Lake (59 °15'N, 114 °09'W), *Picea* arrived slightly later, at 9500 yr BP (~10,600 cal yr BP) and 8800 yr BP (~ 9800 cal yr BP), respectively (MacDonald 1984). It is present at the base of the base of a pollen sequence recovered from John Klondike Bog (60 °20'N,123 °39'W; Matthews 1980), dated to 9600 yr BP (~10,700 cal yr BP). These early forests were dominated by *Picea glauca*, with *P. mariana* underrepresented compared to modern pollen spectra (MacDonald 1987a;b).

According to Vance (1986) maximum warmth and aridity had passed by 9000 yr BP (~10,200 cal. yr BP), although conditions remained warmer and drier than they are at present for several thousand years. Seeds of *Ruppia*, a taxon indicative of hypersaline conditions, disappear from the macrofossil record of Wood Bog (55 °15'N, 118 °72'W; Figure 3.1) about 9200 yr BP (~10,300 cal yr BP; Beaudoin *et al.* 1996). However, at Otasan Lake in the Birch Mountains of northeastern Alberta (57 °42'N 112 °23'W; Figure 3.1), diatom numbers are low between 8200 and 7300 yr BP (~9200 - 8100 cal yr BP), with predominantly benthic, alkaline taxa that suggest low lake levels and possibly a shorter growing season compared to the present (Prather and Hickman 2000).

The earliest evidence of peat accumulation at Rainbow Lake (10,230 cal. yr BP; core coincides with the end of maximum aridity. The presence of Sphagna characteristic of poor fen or bog conditions in basal samples from cores 8 and 10

(9140 cal. yr BP) is surprising, particularly since they are succeeded by what appear to be more minerotrophic taxa in both cases. Assuming that the ecology of these taxa has not changed during the Holocene, their presence in early peat-forming communities suggests that the hydrological framework that created and maintains the present fen areas had not been established at this point. Certainly by the time core 3 initiated (8010 cal. yr BP), however, monocot-dominated communities were present at all three sites.

According to basal depth simulations, (Figure 3.8b-f), small areas of deep peat such as those at coresites 8, 10 and 3 are scattered throughout the study area, and it is likely that several were missed by the depth survey. Since the peat surface was not leveled, present peat depth is not a direct measure of the morphometry of the underlying mineral basin. These isolated areas of deep peat, however, are likely to represent topographic depressions that allowed water to accumulate and served as early foci for peat accumulation. Thus, by 8000 cal. yr BP, peat accumulation at Rainbow Lake was well underway, and marshes or monocot fens occupied several isolated basins within the site.

8000 - 4000 cal. yr BP

Pollen data from Eaglenest Lake suggest that *Pinus* arrived about 7500 yr BP (~8300 cal. yr BP), and that vegetation has been essentially modern since that time (Vance 1986). MacDonald (1987a) found pollen spectra similar to southern boreal forest at Lone Fox, Yesterday and Snowshoe Lakes between 8000 and 6000 yr BP (8800-6800 cal. yr BP), although *Pinus* was still expanding. Modern vegetation established at these sites between 6000 and 5000 yr BP (6800-5700 cal. yr BP), with a similar value estimated for Wild Spear Lake (MacDonald 1984). Since the study area is located in the centre of the boreal forest region, i.e., far from major ecotonal boundaries, lack of vegetation change does not necessarily imply climatic stability. At Boone and Spring Lakes (55 °34'N, 119 °26'W and 55 °34'N, 119 °35'W, respectively; Figure 3.1) modern vegetation did not establish until 5000 yr BP (5700 cal. yr BP; White and Mathewes 1986), and effects of early Holocene aridity were still apparent in

central and southern Alberta until 3000 yr BP (~3200 cal. yr BP; Ritchie and Harrison 1993; Schweger and Hickman 1989; Halsey *et al.* 1998).

Syntheses of available data (Ritchie and Harrison 1993; Vance *et al.* 1995) suggest that temperatures in northwestern Alberta had decreased to modern or near-modern levels by 6000 yr BP (~6800 cal. yr BP), although conditions were probably still drier than today. In contrast to this, Zoltai (1995) suggested mean annual temperatures about 5 ℃ higher than today based on the northward displacement of permafrost zones at 6000 yr BP. At Otasan Lake, the abundance of planktonic diatoms increased between 7300 and 5000 yr BP (~8100 - 5700 cal yr BP), suggesting rising lake levels. Between 5000 and 3100 yr BP (~5700 - 3300 cal yr BP), the flora became dominated by acidophilous taxa, most likely reflecting expansion of the neighbouring peatland (Prather and Hickman 2000).

At the Rainbow Lake peatland, extensive change occurred between 8000 and 4000 cal. yr BP. Basal peat dates suggest that most of the present peatland area originated during this time. *Picea mariana*, *Sphagnum* and ericaceous palynomorphs become more frequent in the regional pollen record and reach modern levels by 4000 yr BP (~4500 cal. yr BP; MacDonald 1987a, b). Cores from this period fall into two distinct categories: Cores 1, 2, 4 and 11 originated by paludification resulting from increased ground- or surface water input. Initial communities were woody or shrubby rich fens, and (disregarding the effects of the 1971 fire) little vegetation change has occurred over time except at coresite 2 which is presently occupied by a *Sphagnum*-dominated poor fen. Peatland initiation at the three shallow plateau sites (nos. 5, 6, and 7) was the result of *Sphagnum* invasion into upland forest. All three cores have been dominated by *Sphagnum* throughout their development, indicating isolation from geogenous water input, most likely because these sites occupy topographically higher positions than the fen areas. Alternatively, fen sites may be associated with coarse-grained substrates that allow for local groundwater discharge. Mineral material recovered during probing often contained sand, making groundwater discharge a possibility. Both scenarios are plausible but untestable given the data available

Permafrost probably first developed at the site between 8000 and 4000 cal. yr BP. The exact point of permafrost initiation within a peat core is hard to determine, and dates quoted in the literature are usually estimates based on either oxygen isotopes (e.g., Vardy *et al.* 1997) or the timing of major changes in macrofossil composition, such as the establishment of hummock Sphagna. Because of its insulative effect, *Sphagnum* is generally regarded as a prerequisite for permafrost initiation in the discontinuous zone (Zoltai *et al.* 1988; Kuhry 1998; Robinson and Moore 2000). Field evidence indicates that permafrost lenses develop in areas of *Sphagnum* peat that are raised above the water table (Zoltai 1993; Robinson and Moore 2000), and such areas are likely to be colonized by trees. Snow interception by tree branches leads to increased frost penetration in winter, and the shaded microclimate prevents permafrost melt in summer (Zoltai 1972; Camill 2000). Camill (2000) found presence of *Picea mariana* to be a prerequisite for permafrost initiation at the local scale in the discontinuous zone of northern Manitoba.

Zoltai's (1993) estimate of 3700 yr BP (~4000 cal. yr BP) for permafrost initiation in peatlands of northwestern Alberta was based on the earliest occurrence of sylvic (charcoal / lichen) peat followed by a *Sphagnum riparium* collapse surface. This date (Rainbow 18-3 in Zoltai 1993) is a minimum estimate, representing the earliest recorded evidence of a burned peat plateau, not permafrost aggradation. The core dated was taken within 10 km of this study and contains about 50 cm of *Sphagnum fuscum* peat underneath the sylvic layer. Ignoring effects of compaction and assuming (a) that about 30 cm of *S. fuscum* peat are required for permafrost initiation, and (b) that peat accumulation from the date of permafrost initiation to the level of Rainbow 18-3 occurred at the same rate as accumulation between Rainbow 18-3 and the next dated sylvic layer (Rainbow 18-2), a maximum estimate for the date of permafrost aggradation is about 5650 cal. yr BP. While this is probably too old, the calculations highlight the uncertainties associated with estimating dates for permafrost initiation from stratigraphic evidence: if accumulation rates are low, small uncertainties regarding stratigraphic depth can lead to large differences in estimated dates.

All dates obtained in this study represent basal peat, and it is unknown when succession to *Sphagnum* occurred in the deep plateau areas. Sphagna were present at the site very early, as shown by the date of 7310 cal. yr BP for basal *S. fuscum / capillifolium* peat at coresite 7. Whether *Sphagnum* had replaced the monocot fen communities in the deep peat basins at this point is unclear. However, if the layer of robust woody roots and *Picea* needles at 220 cm depth in core 8 was deposited on a peat plateau, permafrost initiation occurred rapidly after *Sphagnum* establishment

This interpretation of the data (permafrost initiation concomitant with *S. fuscum / S. capillifolium* establishment) is consistent with published studies (e.g. Couillard and Payette 1985; Zoltai 1995; Kuhry 1998; Oksanen *et al.* 2001). If presence of *Sphagnum* (and trees) is a prerequisite for permafrost formation, absence of suitable *S. fuscum*- or *S. capillifolium*-dominated terrain may have prevented permafrost establishment in the early Holocene. This may explain discrepancies between paleotemperature reconstructions based on permafrost zonation (Zoltai 1995) and those based on palynological evidence (Ritchie and Harrison 1993; Vance *et al.* 1995; see above). However, given the difficulties involved in inferring the timing of permafrost initiation from macrofossil data (Oksanen *et al.* 2001), it is also possible that *Sphagnum*-dominated communities existed at the site for some time before permafrost became established. By 4000 cal. yr BP, permafrost was probably present in many of the current plateau regions, except for shallow areas such as coresites 5 and 6 where organic matter depth may have been insufficient to support permafrost initiation

4000 cal. yr BP - present

There is little evidence for environmental change at the Rainbow Lake site over the last 4000 years. Peat accumulation continued, albeit probably at a slower rate than in the preceding millennia (see below). The only core that initiated during this period is no. 9 from the marginal swamp area, with a basal date of 2120 cal. yr BP at 45-49 cm depth. The present environment at this site is probably similar to conditions at coresites 1, 2, 4, and 11 when these first started accumulating peat. Thus, 'paludifying

forest' may be a more accurate designation for this area, although it is unclear if paludification is actively progressing at this time.

Hydrological relationships between marginal swamp areas and the peatland itself seem worthy of future attention. Paludification usually results from the expansion of existing peatland areas (Aario 1932). The lack of recent basal dates after apparently rapid expansion between 8000 and 4000 cal. yr BP may indicate topographic constraints, such as steepening substrate gradients (Korhola 1994; Almquist-Jacobson and Foster 1995) or increased drainage once water tables built up to the level of an existing outflow. Alternatively, the apparent lack of recent expansion may be related to decreased *vertical* accumulation rates: Peat buildup can impede drainage and raise local or even regional water tables, promoting further paludification (Aario 1932; Kulczynski 1949; Ivanov 1981).

Efficacy of macrofossil data in paleoenvionmental reconstruction

Differential decomposition of taxa has been well documented in litter bag studies and is usually attributed to differences in organic matter quality. (e.g. Johnson and Damman 1991; Belyea 1996; Szumigalski and Bayley 1996). While it is unclear if differences in decay potential at the surface directly translate into differential representation in the peat profile (Latter *et al.* 1998), the possibility of such effects hinders direct comparisons between macrofossil assemblages and modern communities. Paleoenvironmental reconstruction using indicator species can nevertheless be a successful strategy (e.g., Kuhry *et al.* 1993; Janssens *et al.* 1992; Chapter 2) because gradients that control peatland vegetation are well documented, and many peatland bryophytes have narrow tolerances along these gradients, i.e. are good indicators of environmental conditions (e.g., Andrus *et al.* 1983; Andrus 1986; Gignac 1992; Nicholson and Gignac 1995).

On mature permafrost plateaus, peatland bryophytes are replaced by boreal forest taxa such as *Hylocomnium splendens, Pleurozium schreberi, Dicranum* spp. and lichens (mainly *Cladina* and *Cladonia* spp). Except for lichen fragments associated with charcoal layers, these taxa were not recovered from macrofossil samples,

presumably due to poor preservation on the dry plateau surface. Peat formed under permafrost conditions is dominated by woody remains that are not restricted to permafrost environments and have poorly defined taxonomic affinity. Consequently, samples from opposite ends of the upland / peatland / permafrost gradient have similar macrofossil composition, which is reflected in both clustering results (Table 3.1) and the lack of clear environmental gradients in the ordination diagram (Figure 3.14). Macrofossil evidence from peat deposits may be inconclusive if gradients examined include environments where bryophytes are absent or preserve poorly. While interpretation is usually possible in stratigraphic context, quantitative paleoecological evaluation by comparison to surface analogues may be impossible.

Peat charcoal content

Several lines of evidence suggest that regional fire frequency was higher in recent millennia than in the early Holocene. Charcoal records from nearby lake basins suggest low fire activity in the early Holocene and increase to modern levels by approximately 6000 yr BP (~6800 cal. yr BP). At the same time, fire-tolerant conifers (*Pinus contorta* and *Picea mariana*) become increasingly abundant in the regional pollen record (MacDonald 1987a). Variables identified as significant by multiple logistic regression suggest that increased fire frequency was a result of vegetation change, i.e. development of permafrost peat plateaus with dense tree cover and dry, lichen-dominated understorey. This is consistent with reconstructed fire-return rates for permafrost versus non-permafrost sites (Kuhry 1994; Zoltai *et al.* 1998; Robinson and Moore 2000), but it is not the only possible interpretation of the data. Differential preservation, rather than effects of vegetation on fire frequency, may partially explain the results. Woody charcoal may preserve better and is easier to identify reliably than charred moss or herbaceous remains. Likewise, lichen remains were rare in the dataset, but, when present, always associated with at least some charcoal. This suggests that lichens are unlikely to be preserved in peat unless they are rapidly submerged below the water table as a result of fire-induced permafrost collapse.

The 2% charcoal cutoff used here may not be the best indicator of local fire events. Kuhry (1994), for example, observed a minimum charcoal content of 10% in macroscopic charcoal layers. Only 12 samples collected in this study contained this much charcoal, which was deemed insufficient for multivariate analysis. Use of a higher cutoff would have required deliberate sampling of charcoal layers rather than sampling at regular intervals along cores. It is likely that some of the events examined here represent crown fires or airborne contamination from adjacent upland fires. Such contamination, however, would obscure relationships between local vegetation (or macrofossil composition) and the presence of charcoal rather than create them.

Long-term rates of peat accumulation

While it is unclear which model best describes the relationship between peat depth and basal age (Figure 3.16a), long-term apparent rates of peat accumulation increase with core age, a pattern consistent with decreasing rates of vertical accumulation over time. Given the apparently active peat buildup after the 1971 fire, the non-recent age for surface peat predicted by the linear model seems unrealistic, although there may be marked discontinuities in the age/depth relationship of individual cores associated with this (and other) fire events. No attempt was made to date peat immediately underneath the charcoal to determine how many years of accumulation were lost. Robinson and Moore (1999) estimated an average 2.74 cm decrease in vertical accumulation due to individual fire events in peat plateau areas, representing about 150 years of accumulation. Turetsky and Wieder (2001) observed an average organic matter loss of 5.74 $kg \cdot m^2$ (5.74 cm of vertical growth, assuming an average organic matter density of 0.1 $g \cdot cm^3$) in two permafrost bogs in northern Saskatchewan, with a maximum loss of 18.14 $kg \cdot m^2$ for an individual plot. Zoltai *et al.* (1998) estimated an average loss of 13.2 cm surface peat during fire events. If accumulation rates are low, these numbers suggest that several centuries of peat buildup may be lost in individual fires.

Disregarding short-term fluctuations associated with permafrost dynamics (Luken and Billings 1983; Camill 1999; Robinson and Moore 2000; Turetsky *et al.*

2000) permafrost peatlands are generally thought to accumulate peat more slowly than non-permafrost sites. Permafrost aggradation elevates the surface peat well above the water table and may lead to increased fire frequencies (Zoltai *et al.* 1998; Robinson and Moore 2000) and susceptibility to decomposition (Zoltai 1991). Almost no data are available on net primary productivity (NPP) in permafrost peatlands (Campbell *et al.* 2000), but cold temperatures and changes in vegetation cover resulting from permafrost development may reduce productivity in peat plateau areas compared to nonpermafrost bogs. The notion of slow peat accumulation in permafrost sites is supported by faster long-term accumulation rates in boreal areas compared to subarctic or arctic sites (Ovenden 1990; Zoltai 1991; Vardy *et al.* 2000), and by non-recent dates for surface or near-surface peat (Zoltai and Tarnocai 1975; Vardy *et al.* 1997; Peteet *et al.* 1998 and references therein).

Decreased vertical accumulation rates in recent times have been observed in several other permafrost peatlands (Vardy *et al.* 2000; Oksanen *et al.* 2001) and are usually at least tentatively attributed to permafrost aggradation. Differential time available for peat accumulation before permafrost development is the most likely explanation for observed discrepancies in apparent long-term accumulation rates between deep and shallow plateau cores (Figure 3.16b). In fen cores that never contained permafrost (nos. 4, 1, 11 and probably 2), differences in accumulation rates most likely relate to hydrologic constraints, such as differential water input or water table stability.

Overall, the results of this study suggest that effects of widespread permafrost degradation (as may result from climatic change) on the carbon dynamics of peatlands in the discontinuous permafrost zone of northern Alberta will be complex. While initial organic matter accumulation in wet collapse areas is generally high (Camill 1999; Turetsky *et al.* 2000), confounding factors such as changes in seasonal drainage patterns or altered fire frequencies have profound implications for peatland responses at the landscape level.

LITERATURE CITED

Aario L. 1932. Pflanzentopographische und paläogeographische Mooruntersuchungen in N-Satakunta. *Fennia* 55:1-179.

Almquist-Jacobson H and Foster DR. 1995. Toward an integrated model for raised-bog development: Theory and field evidence. *Ecology* 76:2503-2516.

Anderson LE. 1990. A checklist of *Sphagnum* in North America north of Mexico. *The Bryologist* 93:500-501.

Anderson LE, Crum HA and Buck WR. 1990. List of the mosses of North America north of Mexico. *The Bryologist* 93:448-499.

Anderson PM, Barnosky CW, Bartlein PJ, Behling PJ, Brubaker L, Cushing EJ, Dodson J, Dworetsky B, Guetter PJ, Harrison SP, Huntley B, Kutzbach JE, Markgraf V, Marvel R, McGlone MS, Mix A, Moar NT, Morley J, Perrott RA, Peterson GM, Prell WL, Prentice IC, Ritchie JC, Roberts N, Ruddiman WF, Salinger MJ, Spaulding WG, Street-Perrott FA, Thompson RS, Wang PK, Webb T III, Winkler MG and Wright HE Jr. 1988. Climatic changes of the last 18,000 years: Observations and model simulations. *Science* 241:1043-1052.

Andrus RE. 1986. Some aspects of *Sphagnum* ecology. *Canadian Journal of Botany* 64:416-426.

Andrus RE, Wagner DA and Titus JE. 1983. Vertical zonation of *Sphagnum* mosses along hummock-hollow gradients. *Canadian Journal of Botany* 61:3128-3139.

Bayrock LA. 1960. Appendix - Surficial Geology. Pages 43-45 in: Lindsay JD, Pawluk S and Odynsky W. *Exploratory Soil Survey of Alberta Map sheets 84-J, 84-K, and 84-L*. Research Council of Alberta. Edmonton, Alberta.Beilman DW, Vitt DH and Halsey LA. 2001. Localized permafrost peatlands in western Canada: Definition, distributions, and degradation. *Arctic, Antarctic and Alpine Research* 133:70-77.

Beaudoin AB, Wright M and Ronaghan B. 1996. Late Quaternary landscape history and archaeology in the 'Ice-Free Corridor': some recent results from Alberta. *Quaternary International* 32:113-126.

Belyea LR. 1996. Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. *Oikos* 77:529-539.

Birks HJB and Gordon AD. 1985. *Numerical Methods in Quaternary Pollen Analysis*. Academic Press. London.

Borneuf D and Pretula B. 1980. *Hydrogeology of the Zama-Bistcho Lakes Area, Alberta*. Earth Sciences Report: 80-83. Alberta Research Council. Edmonton, Alberta.

Brown RJE. 1968. Occurrence of permafrost in Canadian peatlands. Pages 174-181 in: *Proceedings of the Third International Peat Congress*, Québec, Canada 1968.

Camill P. 1999. Peat accumulation and succession following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Écoscience* 6:592-602.

Camill P. 2000. How much do local factors matter for predicting transient ecosystem dynamics? Suggestions from permafrost formation in boreal peatlands. *Global Change Biology* 6:169-182.

Campbell C, Vitt DH, Halsey LA, Campbell ID, Thormann MN and Bayley SE 2000. *Net primary production and standing biomass in northern continental wetlands.* Information Report NOR-X-369. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta.

Canadian Climate Program. 1993. *Canadian Climate Normals 1961-1990.* Environment Canada, Atmospheric Environment Service.

Chee W-L and Vitt DH. 1989. The vegetation, surface water chemistry and peat chemistry of moderate-rich fens in central Alberta, Canada. *Wetlands* 9:227-262.

Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117-143.

Couillard L and Payette S. 1985. Évolution holocène d'une tourbière à pergélisol (Québec nordique). *Canadian Journal of Botany* 63:1104-1121.

Crum HA and Anderson LE. 1981. *Mosses of Eastern North America*. Columbia University Press. New York.

Deutsch CV and Journel AG. 1998. *GSLIB Geostatistical Software Library and User's Guide*. Second Edition. Oxford University Press. New York.

Dufrêne M and Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-366.

Dyke AS and Prest VK. 1987. *Paleogeography of northern North America, 18 000-5000 years ago.* Geological Survey of Canada, Map no. 1703A. Scale1 : 12,500,000.

French HM. 1996. *The Periglacial Environment.* 2nd. Edition Longman. Harlow, Essex.

Gignac LD. 1992. Niche structure, resource partitioning, and species interactions of mire bryophytes relative to climatic and ecological gradients in western Canada. *The Bryologist* 95:406-418.

Gignac LD and Vitt DH. 1990. Habitat limitations of *Sphagnum* along climatic, chemical, and physical gradients in mires of western Canada. *The Bryologist* 93:7-22.

Goovaerts P. 1999. Geostatistics in soil science: state-of-the-art and perspectives. *Geoderma* 89:1-45.

Goovaerts P. 1997. *Geostatistics for Natural Resources Evaluation*. Oxford University

Press, New York.

Halsey LA, Vitt DH and Bauer IE. 1998. Peatland initiation during the Holocene in Continental Western Canada. *Climatic Change* 40:315-342.

Halsey LA, Vitt DH and Zoltai SC. 1995. Disequilibrium response of permafrost in boreal Continental Western Canada to climate change. *Climatic Change* 30:57-73.

Hann BJ. 1990. Cladocera. Pages 98-91 in: Warner BG. (editor). *Methods in Quaternary Ecology.* Geological Association of Canada, St. Johns, Newfoundland.

Heginbottom JA. 1995. Canada - Permafrost. *The National Atlas of Canada.*5th ed. Map no. MCR 4177. Natural Resources Canada, Ottawa.

Isaaks E. 1990. *The Application of Monte Carlo Methods to the Analysis of Spatially Correlated Data.* Ph.D. Thesis. Stanford University, Stanford, CA.

Ivanov KE. 1981. *Water Movement in Mirelands.* Acadamic Press. London.

Janssens JA, Hansen BCS, Glaser PH and Whitlock C. 1992. Development of a raised-bog complex. Pages 189-221 in: Wright HE Jr, Coffin BA and Aaseng NE. (editors). *The patterned peatlands of Minnesota.* University of Minnesota Press. Minneapolis.

Johnson LC and Damman AWH. 1991. Species-controlled *Sphagnum* decay on a South Swedish raised bog. *Oikos* 61:234-242.

Korhola AA. 1994. Radiocarbon evidence for rates of lateral expansion in raised mires in Southern Finland. *Quaternary Research* 42:299-307.

Kuhry P. 1994. The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. *Journal of Ecology* 82:899-910.

Kuhry P. 1998. Late Holocene permafrost dynamics in two subarctic peatlands of the

Hudson Bay Lowlands (Manitoba, Canada). *Eurasian Soil Science* 31:529-534.

Kuhry P, Nicholson BJ, Gignac LD, Vitt DH and Bayley SE. 1993. Development of *Sphagnum* dominated peatlands in boreal continental Canada. *Canadian Journal of Botany* 71:10-22.

Kulczynski MSt. 1949. Torfowiska Polesia: Peat bogs of Polesie. *Mémoires de l'Académie Polonaise des Sciences et des Lettres. Classe des Sciences Mathématiques et Naturelles Serie B: Sciences Naturelles* 15:1-356.

Kutzbach JE and Webb TI. 1993. Conceptual basis for understanding Late-Quaternary climates. Pages 5-11 in: Wright HE, Kutzbach JE, Webb TI, Ruddiman WF, Street-Perrott FA and Bartlein PJ. (editors). *Global Climates since the Last Glacial Maximum*. University of Minnesota Press. Minneapolis.

Latter PM, Howson G, Howard DM and Scott WA. 1998. Long-term study of litter decomposition on a Pennine peat bog: which regression? *Oecologia* 113:94-103.

Legendre P and Legendre L. 1998. *Numerical Ecology*. 2nd edition . Elsevier. Amsterdam.

Lewis FJ, Dowding ES and Moss EH. 1928. The vegetation of Alberta. II. The swamp, moor and bog forest vegetation of central Alberta. *Journal of Ecology* 16:2-70.

Lindsay JD, Pawluk S, and Odynsky W. 1960. *Exploratory Soil Survey of Alberta Map sheets 84-J, 84-K, and 84-L*. Research Council of Alberta. Edmonton, Alberta.

Luken JO and Billings WD. 1983. Changes in bryophyte production associated with a thermokarst erosion cycle in a subarctic bog. *Lindbergia* 9:163-168.

MacDonald GM. 1984. *Postglacial plant migration and vegetation development in the Western Canadian Boreal forest.* Ph.D. Thesis, University of Toronto.

MacDonald GM. 1987a. Postglacial development of the Subalpine-Boreal transition

forest of Western Canada. *Journal of Ecology* 75:303-320.

MacDonald GM. 1987b. Postglacial vegetation history of the Mackenzie river basin. *Quaternary Research* 28:245-262.

Mackay JR. 1970. Disturbances to the tundra and forest tundra environment of the western Arctic. *Canadian Geotechnical Journal* 7:420-432.

Matthews JV Jr. 1980. Paleoecology of John Klondike Bog, Fisherman Lake Region, Southwest District of Mackenzie. *Geological Survey of Canada Paper* 80-22.

McCune B and Mefford MJ. 1999. *PC-ORD. Multivariate Analysis of Ecological Data, Version 4*. MjM Software Design. Gleneden Beach, Oregon, USA.

Moss EH. 1983. *Flora of Alberta*. 2nd Edition. University of Toronto Press. Toronto.

National Wetlands Working Group. 1988. *Wetlands of Canada*. Ecological Land Classification Series No. 24. Sustainable Development Branch, Environment Canada, Ottawa, Ontario, and Polyscience Publications Inc., Montréal, Québec

Nicholson BJ and Gignac LD. 1995. Ecotope dimensions of peatland bryophyte indicator species along gradients in the Mackenzie River Basin, Canada. *The Bryologist* 98:437-451.

Oksanen PO, Kuhry P and Alekseeva RN. 2001. Holocene development of the Rogavaya River peat plateau, European Russian Arctic. *The Holocene* 11:25-40.

Ovenden L. 1990. Peat accumulation in northern wetlands. *Quaternary Research* 33:377-386.

Payette S. 1988. Late-Holocene development of subarctic ombrotrophic peatlands: allogenic and autogenic succession. *Ecology* 69:516-531.

Peteet D, Andreev A, Bardeen W and Mistretta F. 1998. Long-term Arctic peatland

dynamics, vegetation and climate history of the Pur-Taz region, Western Siberia. *Boreas* 27:115-126.

Prather C and Hickman M. 2000. History of a presently slightly acidic lake in northeastern Alberta, Canada as determined through analysis of the diatom record. *Journal of Paleolimnology* 24:183-198.

Reid DR. 1977. *Permafrost in peat landforms in northwestern Alberta*. Chapter 2 in: Reid DE (editor). Vegetation Survey and Disturbance Studies along the proposed Arctic Gas Route. Canadian Arctic Gas Study Ltd. Calgary, AB.

Ricker WE. 1973. Linear Regressions in Fisheries Research. *Journal of the Fisheries Research Board of Canada* 30:409-434.

Ritchie JC and Harrison SP. 1993. Vegetation, lake levels, and climate in Western Canada during the Holocene. Pages 401-414 in: Wright HE, Kutzbach JE, Webb TI, Ruddiman WF, Street-Perrott FA and Bartlein PJ. (editors). *Global Climates since the Last Glacial Maximum*. University of Minnesota Press. Minneapolis.

Robinson SD and Moore TR. 1999. Carbon and peat accumulation over the past 1200 years in a landscape with discontinuous permafrost, northwestern Canada. *Global Biogeochemical Cycles* 13:591-601.

Robinson SD and Moore TR. 2000. The influence of permafrost and fire upon carbon accumulation in High Boreal peatlands, Northwest Territories, Canada. *Arctic, Antarctic and Alpine Research* 32:155-166.

Rowe RS 1972. *Forest Regions of Canada*. Canadian Forestry Service Publication No. 1300. Department of the Environment, Ottawa

Schweger CE and Hickman M. 1989. Holocene paleohydrology of central Alberta: testing the general-circulation-model climate simulations. *Canadian Journal of Earth Sciences* 26:1826-1833.

Shay JM and Shay T. 1986. Prairie marshes in western Canada, with specific reference to the ecology of five emergent macrophytes. *Canadian Journal of Botany* 64:443-454.

Sjörs H. 1980. An arrangement of changes along gradients, with examples from successions in boreal peatlands. *Vegetatio* 43:1-4.

Sokal RR and Rohlf FJ. 1995. *Biometry.* 3rd Edition. W.H. Freeman and Company. New York.

Stuiver M and Reimer PJ 1993. Extended ^{14}C database and revised CALIB radiocarbon calibration program. *Radiocarbon* 35: 215-230

Stuiver M, Reimer PJ, Bard E, Beck JW, Burr GS, Hughen KA, Kromer B, McCormac G, van der Plicht J and Spurk M. 1998. INTCAL98 radiocarbon age calibration, 24,000-0 cal BP. *Radiocarbon* 40:1041-1083.

Szumigalski AR and Bayley SE. 1996. Decomposition along a bog to rich fen gradient in central Alberta, Canada. *Canadian Journal of Botany* 74:537-581.

Tallis JH. 1983. Changes in wetland communities. Pages 311-347 in: Gore AJP. (editor). *Mires: swamp, bog, fen and moor: General studies.* Ecosystems of the world. 4A. Elsevier Scientific Publishing Company. Amsterdam.

Thie J. 1974. Distribution and thawing of permafrost in the southern part of the discontinuous permafrost zone in Manitoba. *Arctic* 27:189-200.

Turetsky MR and Wieder RK. 2001. A direct approach to quantifying organic matter lost as a result of peatland wildfire. *Canadian Journal of Forest Research* 31:363-366.

Turetsky MR, Wieder RK, Williams CJ and Vitt DH. 2000. Organic matter accumulation, peat chemistry and permafrost melting in peatlands of boreal Alberta. *Écoscience* 7:379-392.

Vance RE. 1986. Pollen stratigraphy of Eaglenest Lake, northeastern Alberta. *Canadian Journal of Earth Sciences* 23:11-20.

Vance RE, Beaudoin AB and Luckman BH. 1995. The paleoecological record of 6 ka BP climate in the Canadian Prairie Provinces. *Géographie physique et Quaternaire* 49:81-98.

Vardy SR, Warner BG, Turunen J and Aravena R. 2000. Carbon accumulation in permafrost peatlands in the Northwest Territories and Nunavut, Canada. *The Holocene* 10:273-280.

Vardy SR, Warner BG and Aravena R. 1997. Holocene climate effects on the development of a peatland on the Tuktoyaktuk Peninsula, Northwest Territories. *Quaternary Research* 47:90-104.

Vardy SR, Warner BG and Aravena R. 1998. Holocene climate and the development of a subarctic peatland near Inuvik, Northwest Territories. *Climatic Change* 40:285-313.

Vitt DH, Halsey LA, Bauer IE and Campbell C. 2000. Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. *Canadian Journal of Earth Sciences* 37:683-693.

Vitt DH, Halsey LA, Thormann MN and Martin T. 1996. *Peatland Inventory of Alberta.* Alberta Peat Task Force, Network of Centres of Excellence in Sustainable Forest Management Grant, University of Alberta, Edmonton, Alberta

Vitt DH, Halsey LA and Zoltai SC. 1994. The bog landforms of continental western Canada in relation to climate and permafrost patterns. *Arctic and Alpine Research* 26:1-13.

Ward JH. 1963. Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* 58:236-244.

Webb III T, Ruddiman WF, Street-Perrott FA, Markgraf V, Kutzbach JE, Bartlein PJ, Wright HEJr and Prell WL. 1993. Climatic changes during the past 18,000 years: regional syntheses, mechanisms, and causes. Pages 514-535 in: Wright HE, Kutzbach JE, Webb TI, Ruddiman WF, Street-Perrott FA and Bartlein PJ. (editors). *Global Climates since the Last Glacial Maximum*. University of Minnesota Press. Minneapolis.

White JM and Mathewes RW. 1986. Postglacial vegetation and climatic change in the upper Peace River district, Alberta. *Canadian Journal of Botany* 64:2305-2318.

Zar JH. 1999. *Biostatistical Analysis*. 4th Edition. Prentice Hall, Upper Saddle River, New Jersey.

Zoltai SC. 1971. Southern limit of permafrost features in peat landforms, Manitoba and Saskatchewan. *The Geological Association of Canada, Special Paper* Number 9:305-310.

Zoltai SC. 1972. Palsas and Peat Plateaus in Central Manitoba and Saskatchewan. *Canadian Journal of Forest Research* 2:291-302.

Zoltai SC. 1991. Estimating the age of peat samples from their weight: a study from west-central Canada. *The Holocene* 1:68-73.

Zoltai SC. 1993. Cyclic development of permafrost in the peatlands of Northwestern Alberta, Canada. *Arctic and Alpine Research* 25:240-246.

Zoltai SC. 1995. Permafrost distribution in peatlands on west-central Canada during the Holocene warm period 6000 years BP. *Géographie physique et Quaternaire* 49:45-54.

Zoltai SC, Morrissey LA, Livingston GP and de Groot WJ. 1998. Effects of fires on carbon cycling in North American boreal peatlands. *Environmental Reviews* 6:13-24.

Zoltai SC and Tarnocai C. 1975. Perennially frozen peatlands in the western Arctic and Subarctic of Canada. *Canadian Journal of Earth Sciences* 12:28-43.

Zoltai SC, Tarnocai C, Mills GF and Veldhuis H. 1988. Wetlands of Subarctic Canada. Pages 55-96 in: National Wetlands Working Group. *Wetlands of Canada.* Ecological Land Classification Series. No. 24. Sustainable Development Branch, Environment Canada, Ottawa, Ontario, and Polyscience Publications Inc., Montréal, Québec.

Table 3.1: Minimum variance cluster groups of macrofossil data, and taxa with significant indicator values for each cluster. RA = Relative abundance (% of total abundance of taxon *j* that occurs within cluster *k*). RF = Relative frequency (% of samples in cluster *k* which contain taxon *j*). IV = Indicator value. Only species with indicator values >20 are shown, except in the case of cluster 1 where the only significant indicator value was <20.

Cluster group	number of samples	indicator species / class	RA (%)	RF (%)	IV	p
1	27	smooth woody roots	51	33	17.0	0.0495
2	25	wood / bark	53	100	52.6	0.0001
		miscellaneous roots	68	44	29.9	0.0033
3	25	herbaceous remains	47	100	46.8	0.0001
4	10	*Sphagnum angustifolium*	75	100	74.8	0.0001
5	20	*Sphagnum riparium*	61	35	21.5	0.0106
6	38	*S. fuscum / capillifolium*	58	100	58.1	0.0001
7	11	robust woody roots	51	100	51.3	0.0001
		Sphagnum warnstorfii	99	45	44.9	0.0003
		Picea mariana	62	36	22.5	0.0080
8	11	*Polytrichum strictum*	96	100	90.1	0.0001

Table 3.2: Univariate regressions of CHARCOAL on depth, macrofossil groups and NMDS axes. Values in the -2LL column represent total deviance of the univariate model, and G (log likelihood ratio) values compare model deviance with deviance of the null model. Sample size is 173 except for NMDS1-3 which exclude surface samples (n=162). Variables that are significant at α=0.05 are flagged with an asterisk (*).

	Coefficient	SE	Wald	p_{Wald}	-2LL	G	p_G
depth*	-0.0069	0.0029	2.427	0.015	155.8	6.928	0.009
log(WOODY+1)*	0.5606	0.1863	3.009	0.003	152.0	10.71	0.001
HERB	-0.0059	0.0063	0.933	0.351	161.8	0.898	0.343
SPHA	-0.0054	0.0057	0.954	0.340	161.7	0.935	0.334
SPHC	-0.0035	0.0090	0.388	0.698	162.5	0.155	0.694
BBRYO.prab	-0.3651	0.6456	0.566	0.571	162.3	0.334	0.563
OBRYO.prab	-1.1307	0.7584	1.491	0.136	159.8	2.857	0.091
LICHEN.prab*	3.0390	1.1342	2.679	0.007	153.1	9.546	0.002
NMDS1	0.2656	0.2854	0.930	0.352	157.3	0.879	0.349
NMDS2	-0.6067	0.3921	1.547	0.122	155.8	2.368	0.124
NMDS3	-0.7986	0.4192	1.905	0.057	154.5	3.703	0.054

Table 3.3: Variables included in the final logistic regression model for CHARCOAL. The number shown for the intercept under -2LL is the deviance of the null model (i.e. the error associated with the model if only the intercept is included). Values of -2LL for log(WOODY+1) and LICHEN.prab denote model deviance with each of these variables removed. Deviance for the full model is 142.68.

	Coefficient	SE	Wald	p_{Wald}	-2LL	G	p_G
intercept	-3.332	0.652	5.112	0.000	162.7	N/A	N/A
log(WOODY+1)	0.576	0.193	2.982	0.003	153.1	10.44	0.001
LICHEN.prab	3.130	1.192	2.625	0.024	152.0	9.28	0.002

Table 3.4: Basal radiocarbon dates and long-term apparent rates of peat accumulation.

Core no.	Lab no.	depth (cm)	$\delta^{13}C$ (‰)	Conventional ^{14}C age	Error* (SD)	Calibrated ^{14}C age (median probability)	Calibrated age range (2σ; Method B)	Apparent rate of peat accumulation (mm/year)
1	GSC 6151	111-118	-29.1	5000	50	5750	5857- 5640	0.20
2	GSC 6153	183-187	-27.2	5410	60	6200	6329 - 6032	0.30
3	GSC 6157	252-256	-29.7	7200	70	8010	8157 - 7869	0.32
4	GSC 6160	29-33	-29.0	3940	50	4390	4497 - 4235	0.07
5	GSC 6163	68-72	-27.1	3770	50	4140	4291 - 3984	0.17
6	GSC 6167	79-83	-27.3	4270	60	4840	4954 - 4639	0.17
7	GSC 6169	100-104	-27.4	6230	60	7130	7278 - 6960	0.14
8	BGS 2114	310-314	-30.0	9065	120	10220	10516 - 9865	0.31
9	BGS 2115	45-49	-28.6	2136	70	2120	2302 - 1941	0.22
10	BGS 2116	295-299	-28.9	8175	90	9150	9444 - 8857	0.32
11	BGS2117	153-157	-29.7	5600	80	6390	6564 - 6239	0.24

* GSC error terms include an error multiplier of 1.6 (McNeely *personal communication*)

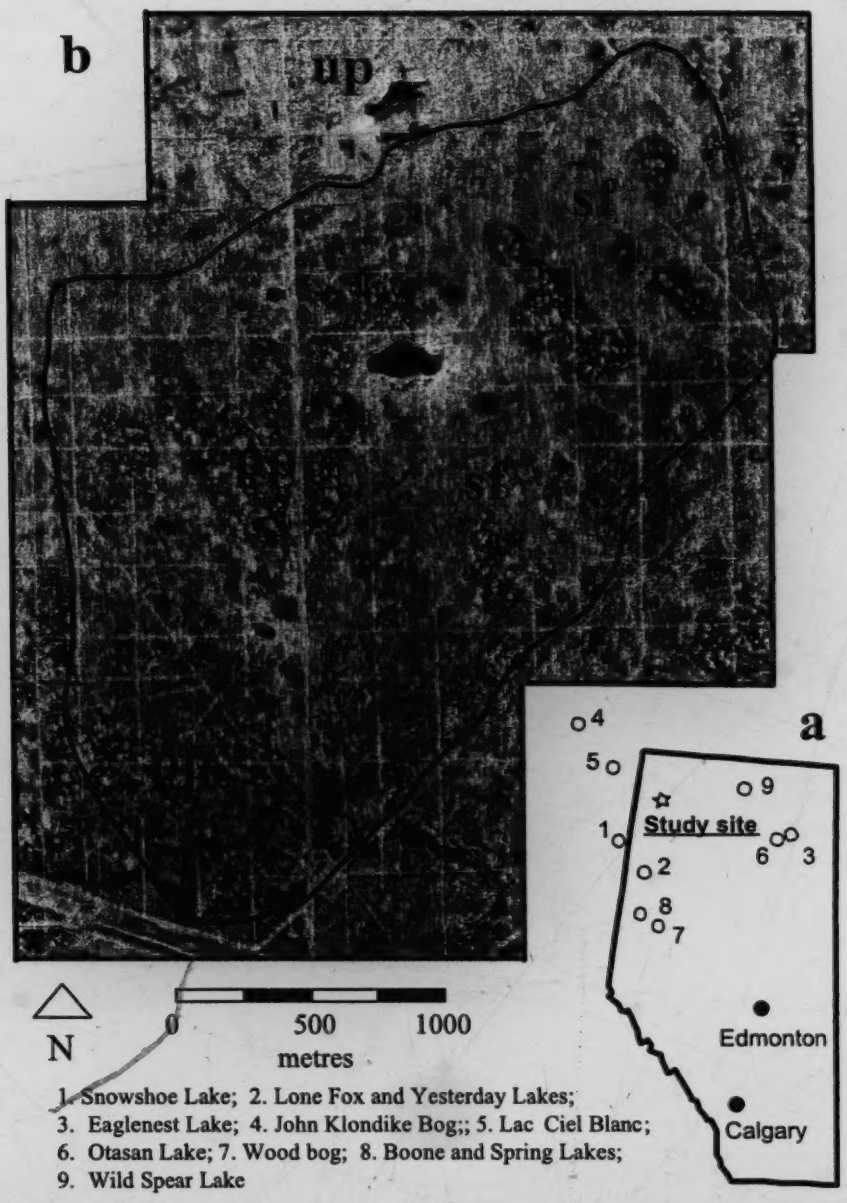


Figure 3.1: **(a)** Location of the study site (star) within Alberta, Canada. Open circles mark paleoecological sites mentioned in the text. **(b)** Aerial photograph of the Rainbow Lake peatland complex. A gravel road crosses the site from north to south, passing to the right of the two small lakes in the left half of the picture; other straight lines are cutlines from seismic exploration. The black solid line represents the study area boundary. **up** = upland; **sf** = shrubby fen; **pp** = (collapsed) peat plateau area. Aerial photographs courtesy of Air Photo Distribution, Government of Alberta; reproduced with permission.

Figure 3.2: Appearance of the former peat plateau regions in 1996. Note dense cover of ericaceous shrubs and herbaceous vegetation.

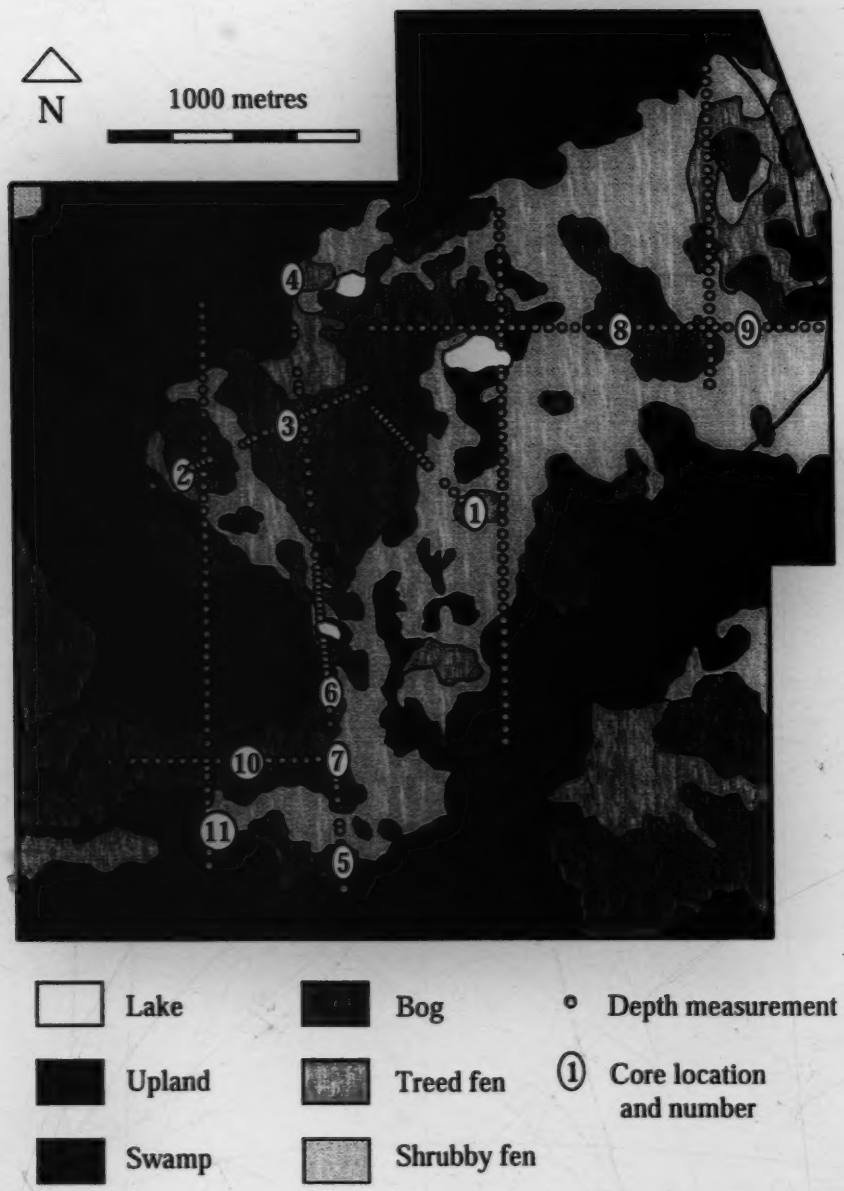


Figure 3.3: Map of the study area, showing main peat landforms, depth survey points, and coring locations. Landform boundaries were mapped from 1:15,000 aerial photographs flown in 1979. (Mapping of wetland classes by L. Halsey; see Appendix 1). Note that, coresite 9, classified here as shrubby fen, is referred to as swamp in the text (see Methods section)..

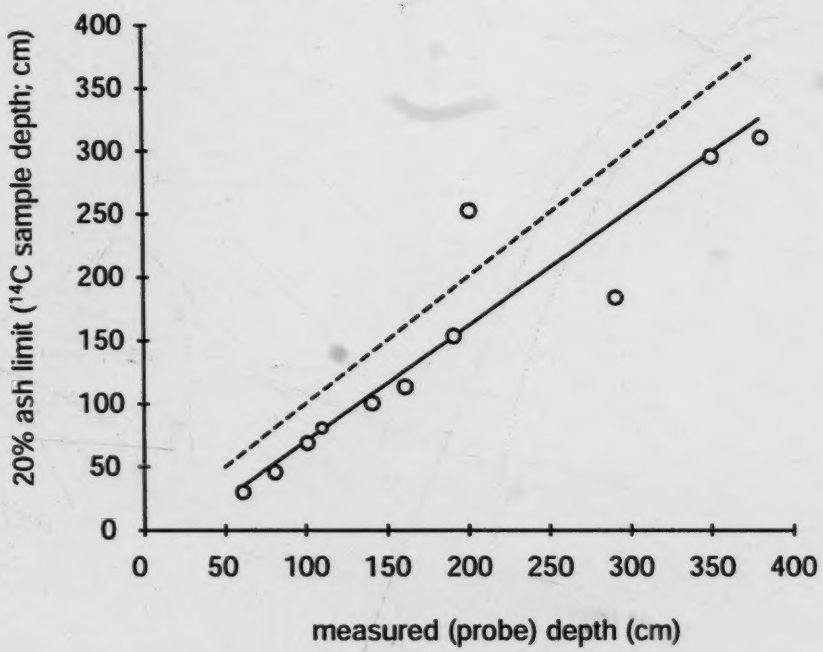


Figure 3.4: Relationship between field measurements of peat depth (probe depth) and basal depth (20% ash limit) at coring locations. The solid line is the functional relationship from Major Axis regression (R^2 = 0.879; p<0.001); The stippled line marks the 1:1 relationship between the two variables, i.e., the line expected if probe depth is an unbiased predictor of basal depth

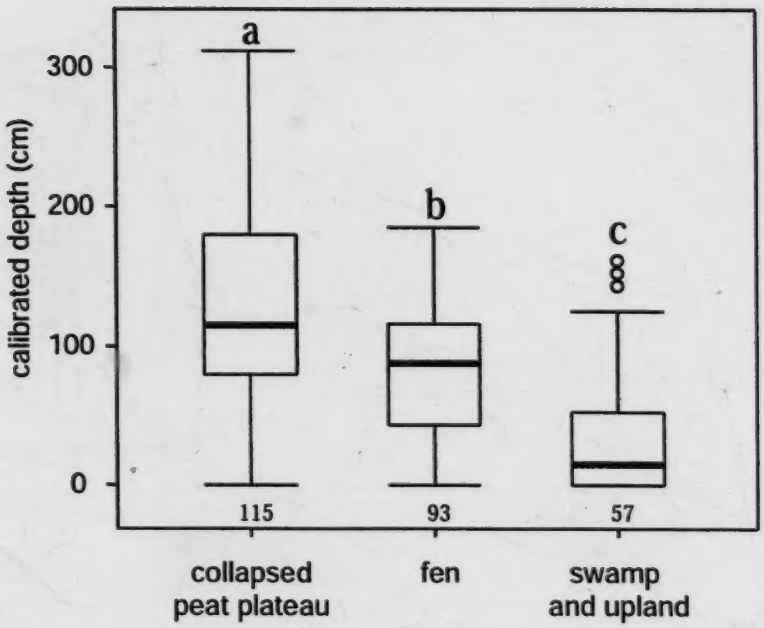


Figure 3.5: Differences in basal depth between landform types. Thick solid lines represent median peat depths for the different landforms. The lower and upper margin of each box mark the position of the 25th and 75th percentiles, respectively, i.e. the height of each box corresponds to the interquartile range. Upper and lower horizontal bars ('whiskers') show the range of data values excluding outliers. Outliers are defined as points that are located more than 1.5 interquartile ranges from the nearest quartile and plotted as open circles. Lower case letters denote groups identified as significantly different by nonparametric multiple comparison (Dunn test; Zar 1999). Numbers at the bottom are sample sizes.

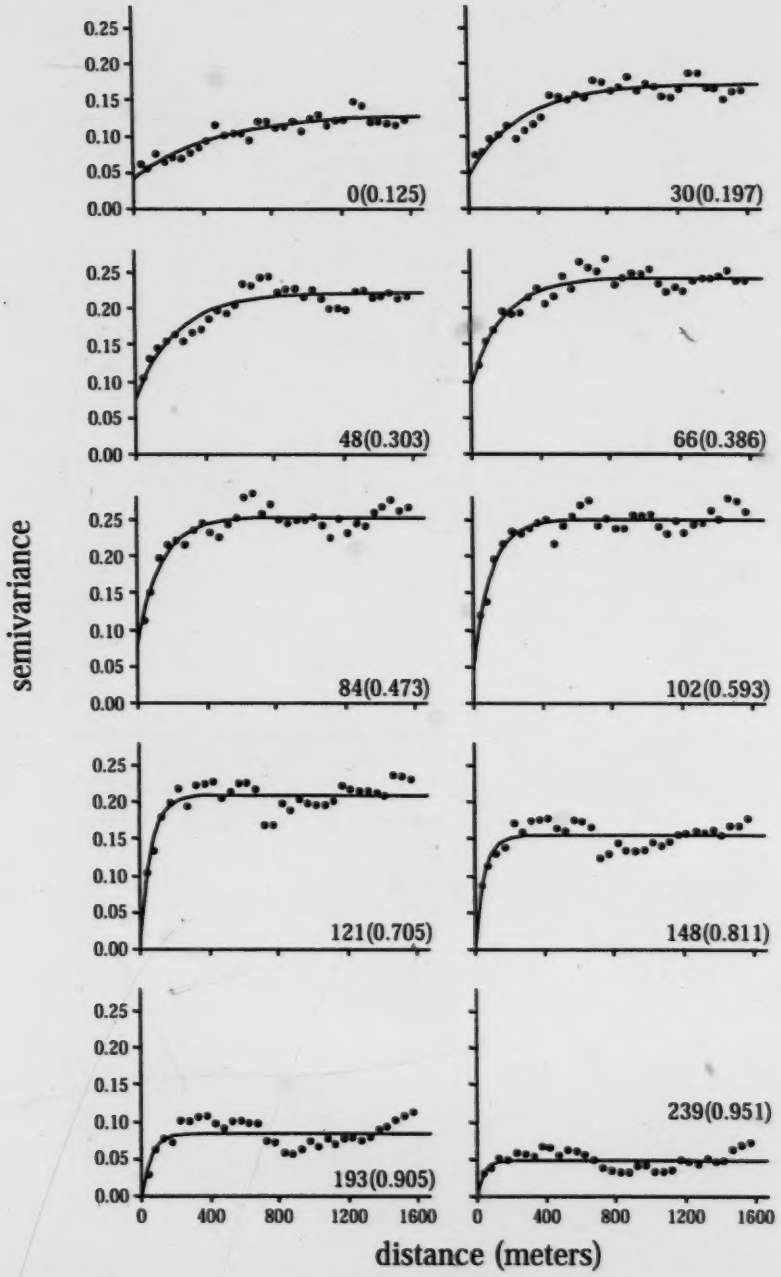


Figure 3.6: Sample variograms and fitted exponential models at ten successive indicator thresholds. The first number on each plot denotes the indicator (depth) threshold shown; the number in brackets shows the corresponding percentile of the input sample. Changes in total semivariance with depth are a result of indicator transformation. Variance is highest close to the sample median because at this point the transformed dataset contains equal numbers of zeroes and ones.

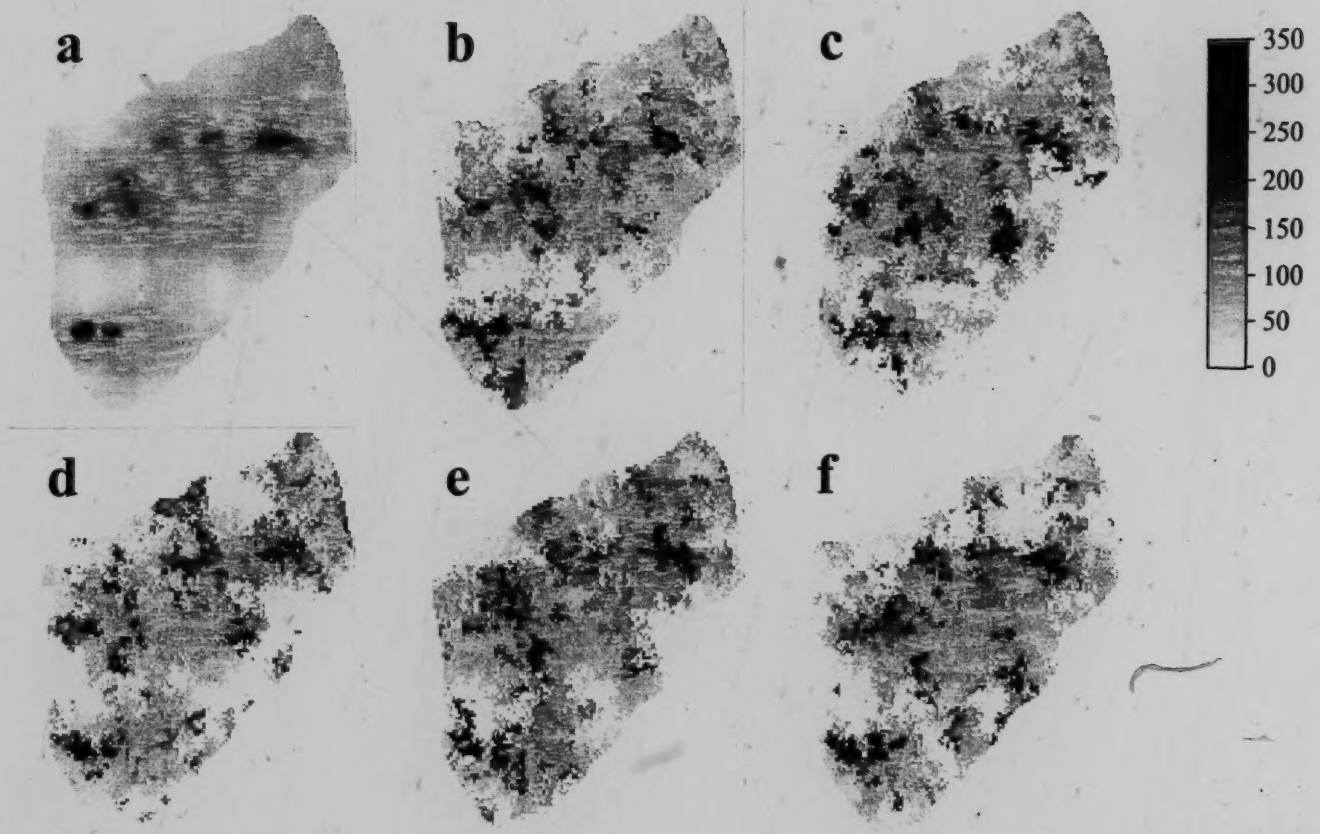
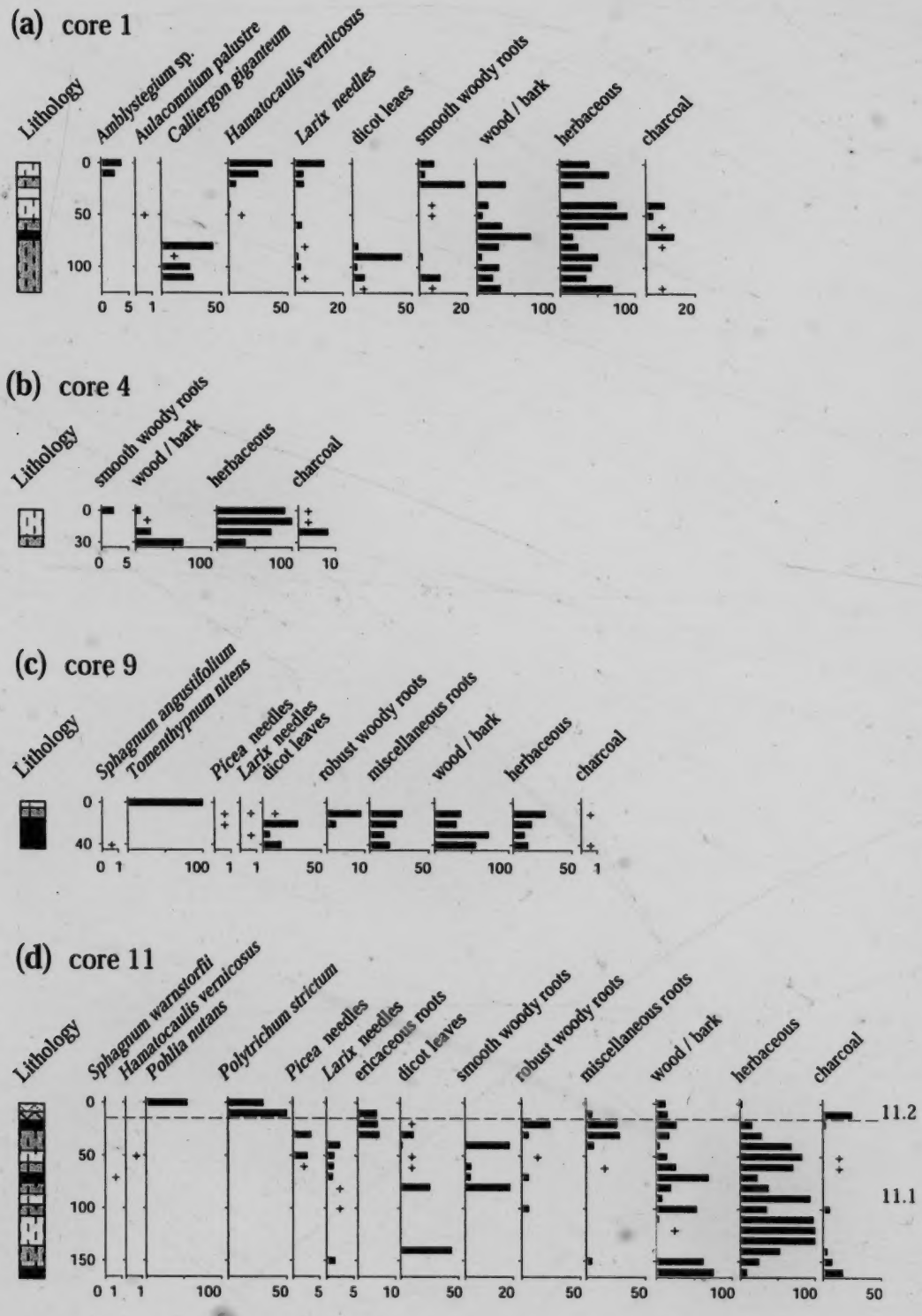


Figure 3.7: **(a)** mean peat depth prediction for each grid node from 500 simulated realizations. There is a marked smoothing effect, with discontinuities at sample locations. **(b) - (f)** Five of the 500 realizations generated by stochastic simulation. Differences between realizations reflect uncertainty associated with individual grid nodes. For further explanation, see text.


(a) core 1
Lithology
Amblystegium sp.
Aulacomnium palustre
Calliergon giganteum
Hamatocaulis vernicosus
Larix needles
dicot leaes
smooth woody roots
wood / bark
herbaceous
charcoal
0
50
100
0 5 1 50 50 20 50 20 100 100 20
(b) core 4
Lithology
smooth woody roots
wood / bark
herbaceous
charcoal
0
30
0 5 100 100 10
(c) core 9
Lithology
Sphagnum angustifolium
Tomenthypnum nitens
Picea needles
Larix needles
dicot leaves
robust woody roots
miscellaneous roots
wood / bark
herbaceous
charcoal
0
40
0 1 100 1 1 50 10 50 100 50 1
(d) core 11
Lithology
Sphagnum warnstorfii
Hamatocaulis vernicosus
Pohlia nutans
Polytrichum strictum
Picea needles
Larix needles
ericaceous roots
dicot leaves
smooth woody roots
robust woody roots
miscellaneous roots
wood / bark
herbaceous
charcoal
0
50
100
150
0 1 1 100 50 5 5 10 50 20 50 50 100 100 50
11.2
11.1

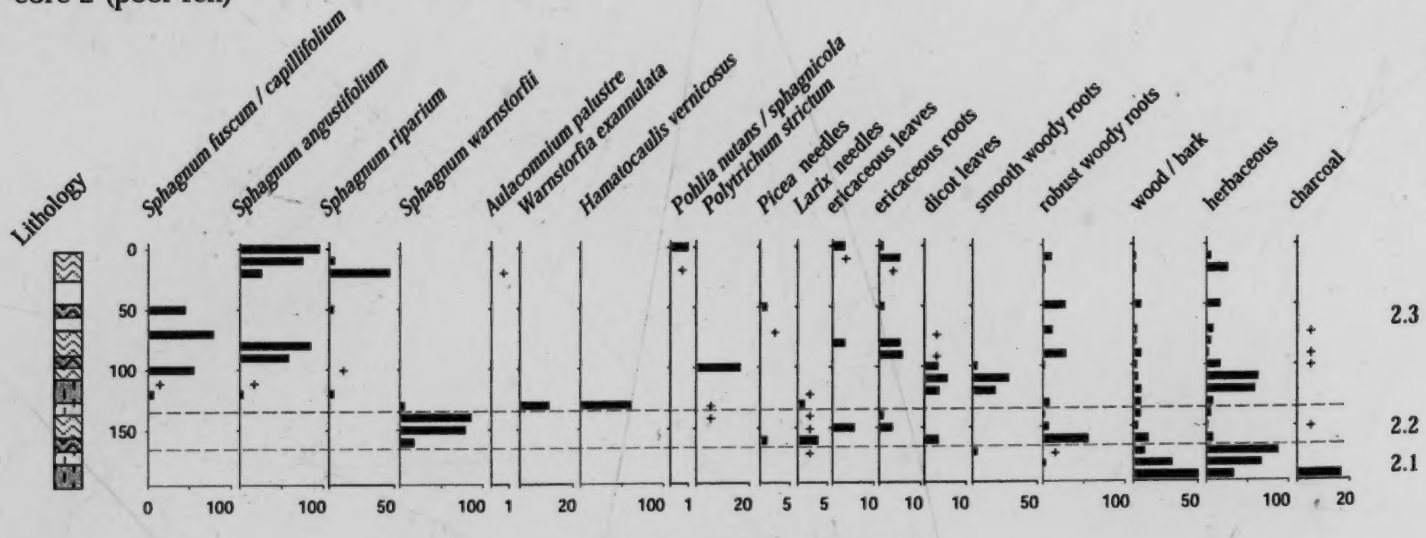


Figure 3.9: Macrofossil diagram for a poor fen core from the Rainbow Lake peatland. For an explanation of symbols, see legend for Figure 3.8

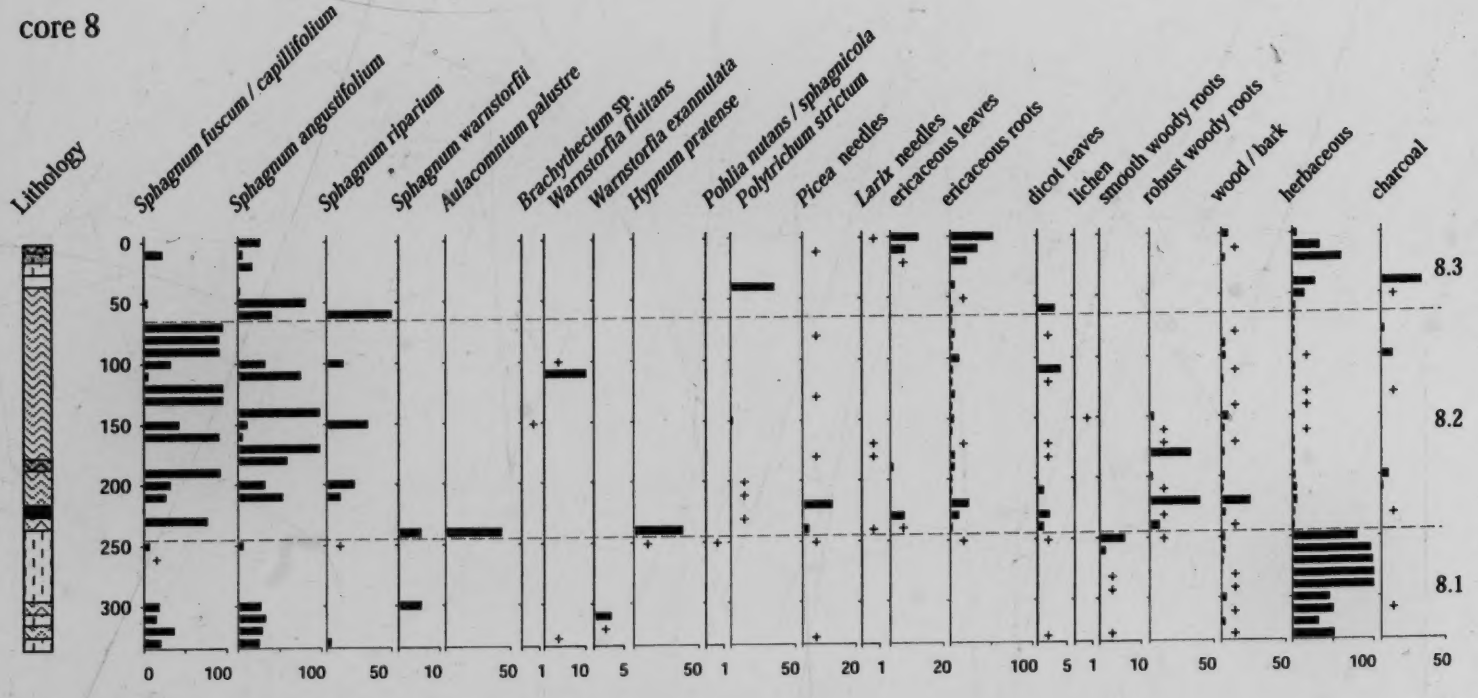


Figure 3.10: Macrofossil diagram for a deep peat plateau core (no. 8) from the Rainbow Lake peatland. For an explanation of symbols, see legend for Figure 3.8

core 10

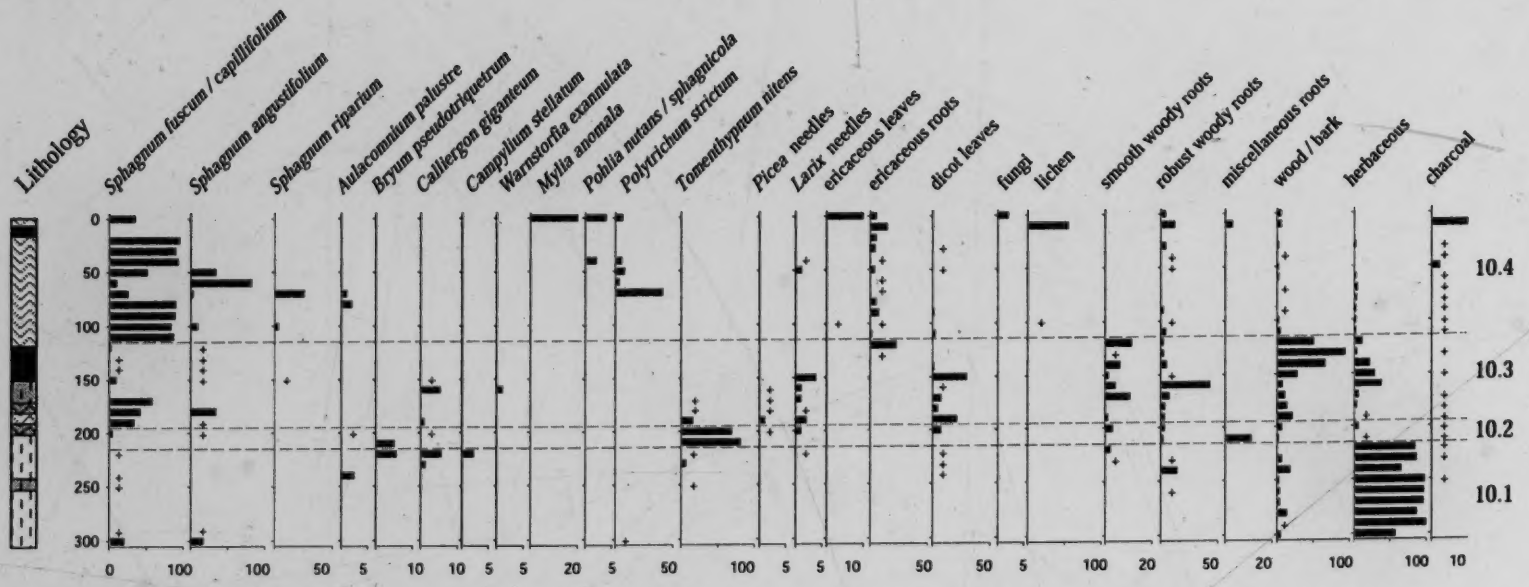


Figure 3.11: Macrofossil diagram for a deep peat plateau core (no. 10) from the Rainbow Lake peatland. For an explanation of symbols, see legend for Figure 3.8

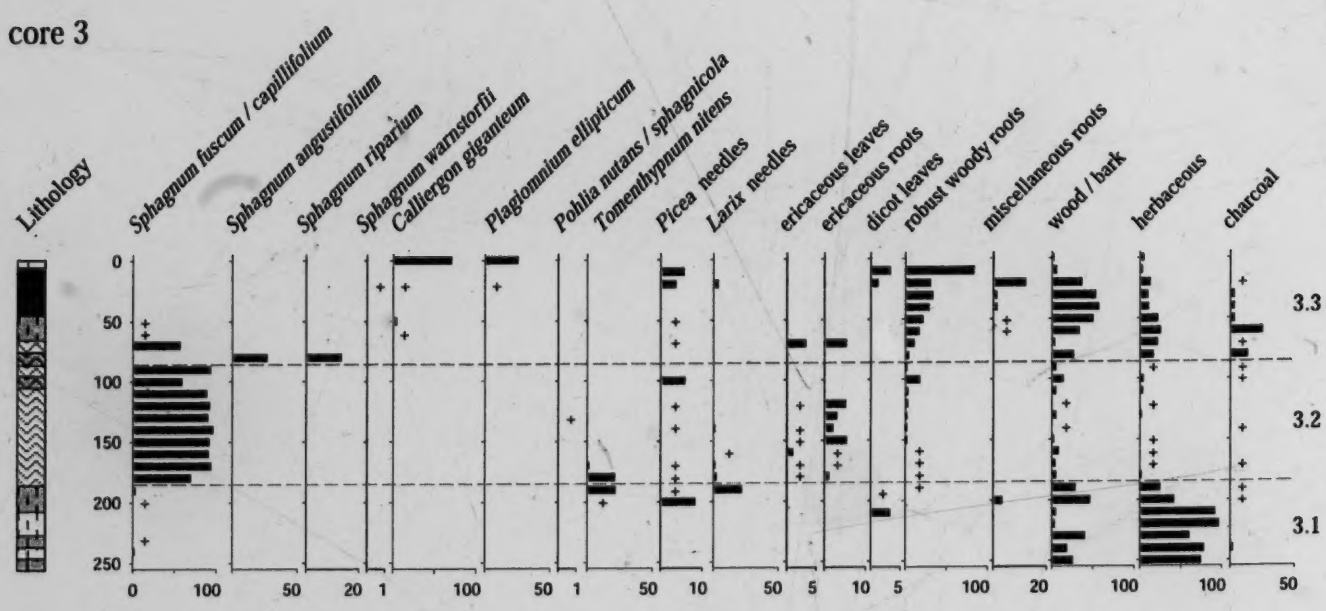


Figure 3.12: Macrofossil diagram for a deep peat plateau core (no. 3) from the Rainbow Lake peatland. For an explanation of symbols, see legend for Figure 3.8

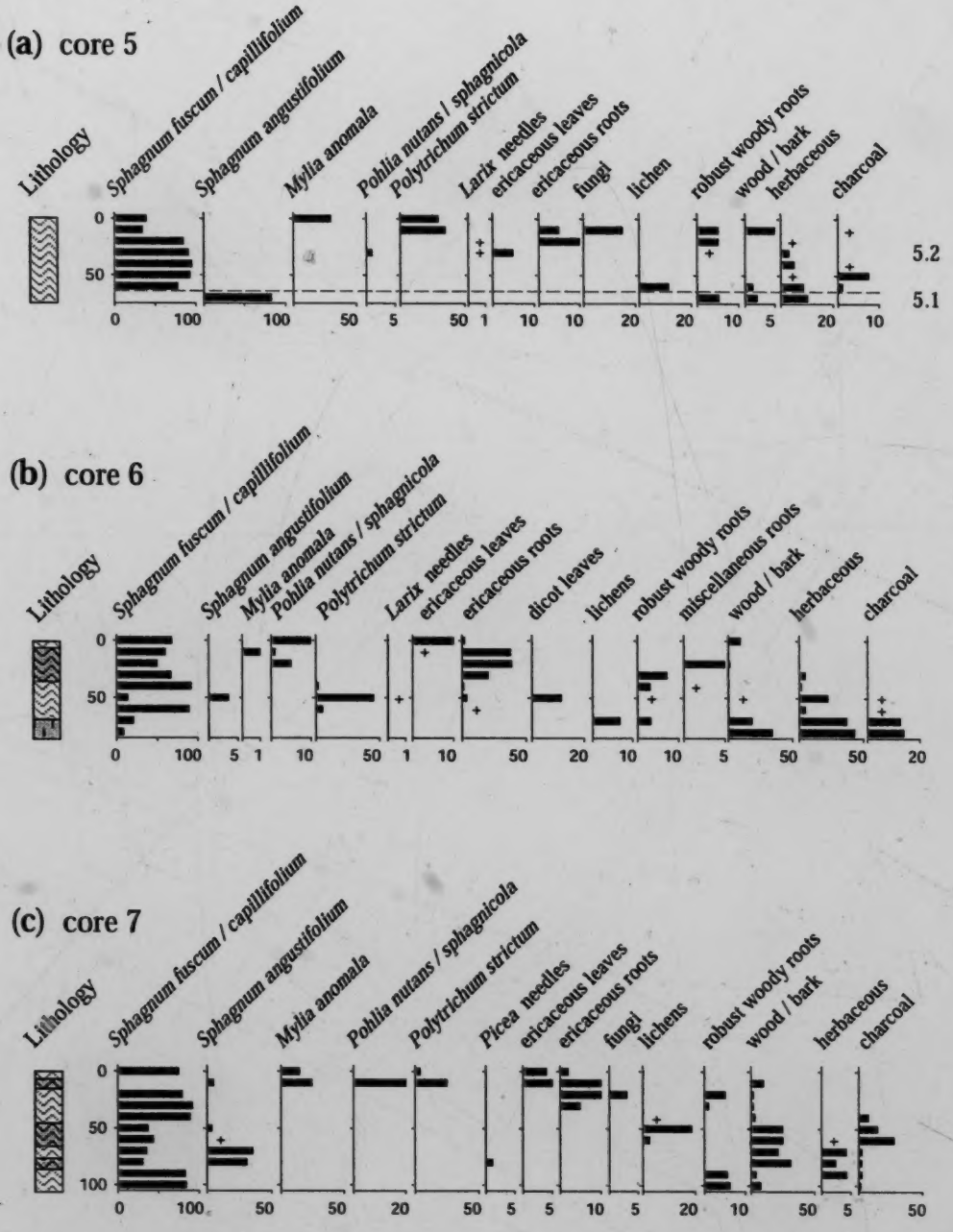


Figure 3.13: Macrofossil diagrams for three shallow peat plateau cores from the Rainbow Lake peatland. For an explanation of symbols, see legend for Figure 3.8

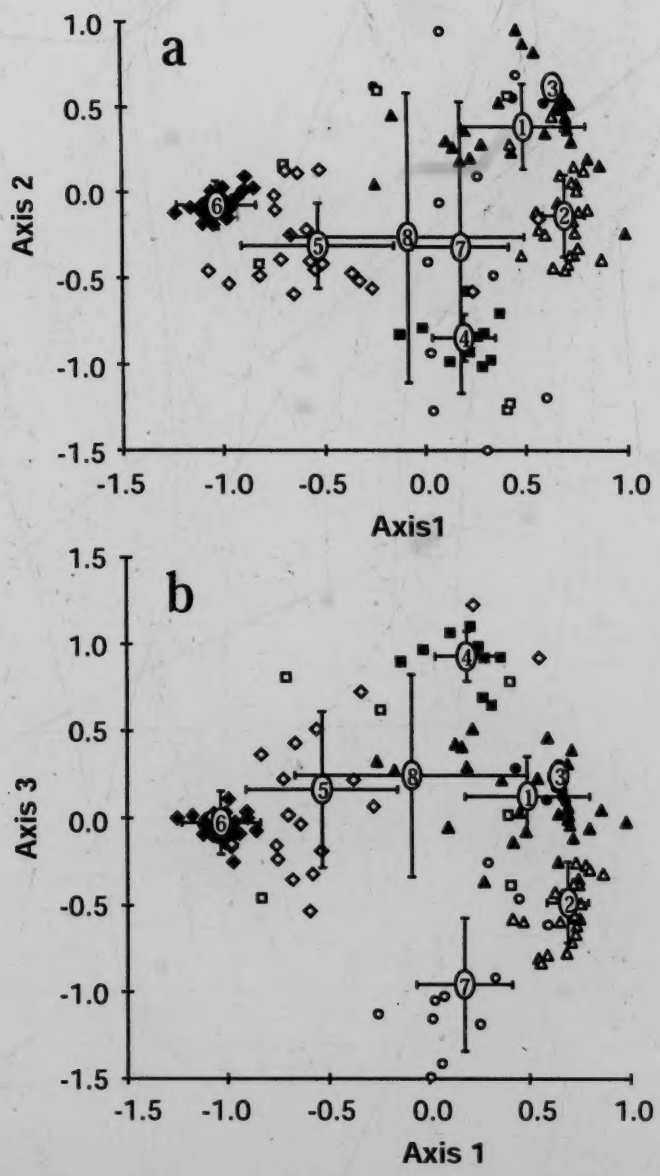


Figure 3.14: NMDS ordination of macrofossil data. (a) Axis 1 and axis 2; (b) axis 1 and axis 3; Numbers mark the bivariate mean (centroid) of minimum variance cluster groups, and error bars correspond to one standard deviation. Symbols and indicator taxa for groups are; (1) ▲ smooth woody roots; (2) △ wood / bark, miscellaneous roots; (3) ● herbaceous remains; (4) ■ *Sphagnum angustifolium;* (5) ◇ *S. riparium;* (6) ◆ *S. fuscum / S. capillifolium;* (7) ○ robust woody roots, *S. warnstorfii, Picea mariana* needles; (8) □ *Polytrichum strictum.* For indicator values and significance levels, refer to Table 3.1

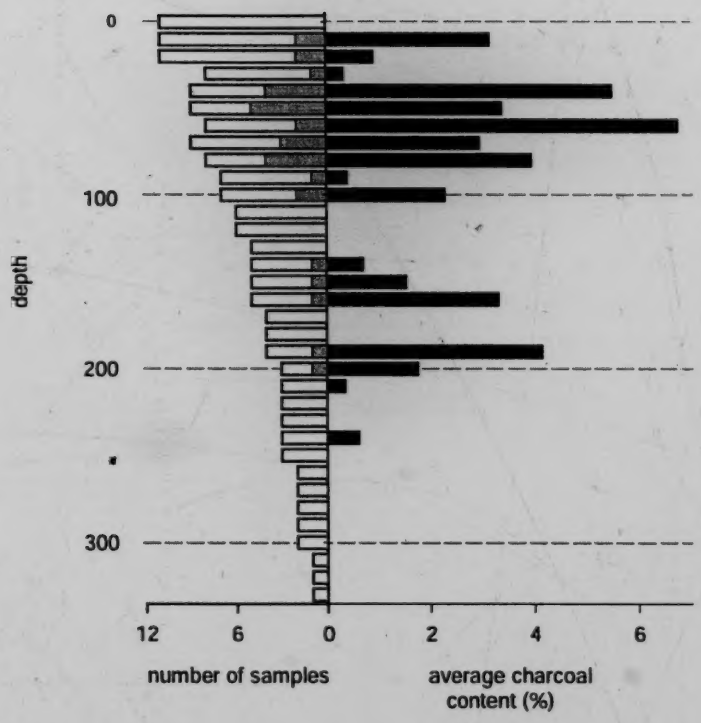


Figure 3.15: Changes in charcoal content with depth in the 173 macrofossil samples. Solid bars plotted on the right show the average charcoal content (% of sample volume) for all samples available from a given depth. Open (white) bars on the left show the total number of samples available from that depth, and shaded (grey) bars indicate the number of samples that contained >2% charcoal.

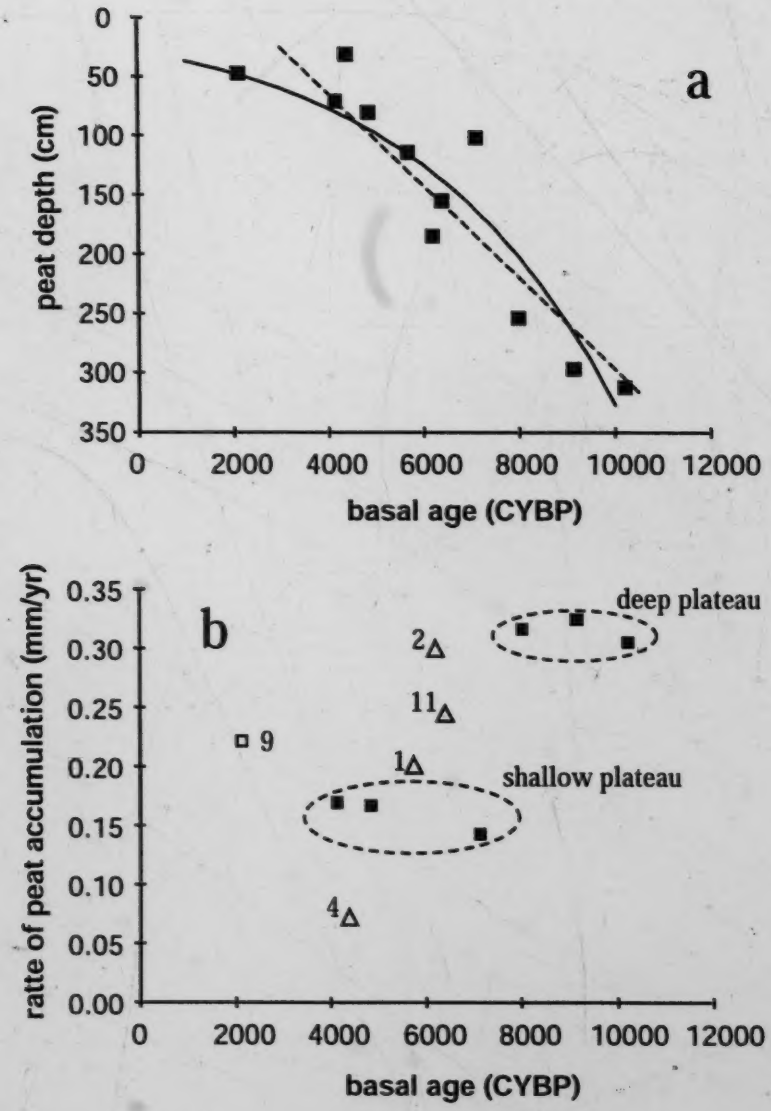


Figure 3.16: (a) Relationship between basal peat age and depth. Linear and exponential models fitted to the points are shown by stippled and solid lines, respectively. (b) Long-term rates of peat accumulation (mm/year) for the 11 cores plotted against basal age. ■ Peat plateau cores; △ fen cores; □ core from marginal swamp area.

CHAPTER 4

Modelling effects of litter quality and environment on organic matter accumulation over different timescales

INTRODUCTION

Since the end of the last glacial period, boreal and subarctic peatlands have accumulated an estimated 270 - 455 petagrams of carbon (1 Pg = 10^{15} g; Turunen *et al.* 2002; Gorham 1991). This represents up to a third of the global soil carbon pool, or two thirds of the amount of carbon contained in the atmosphere during the 1980s (Houghton *et al.* 2001). At present, northern peatlands represent a net sink of atmospheric carbon dioxide (CO_2) and a net source of methane (CH_4; Moore 1994). Effects of climate change on peatland C dynamics are hard to predict and will differ between regions and peatland types (Gorham 1991; Moore *et al.* 1998). Even within the same peatland, source / sink dynamics for CO_2 and CH_4 differ between microsites (Waddington and Roulet 1996; Alm *et al.* 1997), and daily or annual carbon budgets may become negative under certain conditions (Alm *et al.* 1997; 1999). Anticipated changes in regional peatland distribution (Gignac *et al.* 1998), effects of permafrost melt (Kolchugina and Vinson 1993; Camill 1999; Turetsky *et al.* 2000) and likely increases in fire frequency (Kuhry 1994; Zoltai *et al.* 1998; Pitkänen *et al.* 1999) further complicate quantitative predictions.

Peatland carbon dynamics have been measured and compared on a variety of temporal scales, ranging from continuous CO_2 flux measurements (Joiner *et al.* 1999; Lafleur *et al.* 2001), to millennial-scale patterns inferred from peat cores (Warner *et al.* 1993; Tolonen and Turunen 1996; Clymo *et al.* 1998). Measurement of contemporary carbon flux is the most direct way of assessing the influence of local environmental conditions on daily, seasonal or annual C budgets. However, net ecosystem exchange (NEE) reflects the balance between C sequestration at the surface and mineralization throughout the peat column, which implies that the net ability of a peatland to sequester carbon decreases over time (Clymo 1984). This suggests that results of contemporary flux measurements cannot be extrapolated to sites of dissimilar age or depth and should be evaluated within the context of long-term site development.

Over decadal and centennial timescales, climate change is likely to cause marked shifts in peatland distribution and community composition (Gignac and Vitt 1994; Gignac *et al.* 1998). Paleoecological data indicate that peatland extent and distributions have changed dramatically in response to climate change in the past (Halsey *et al.* 1998; Halsey *et al.* 2000), and ecological studies demonstrate that autogenic succession, particularly in combination with anthropogenic effects, can cause marked community change over a few decades (van Diggelen *et al.* 1996; Gunnarsson *et al.* 2000). Community transitions are well-documented in the paleoecological record (e.g. Tolonen 1967; Kuhry *et al.* 1993), even if exact forcing mechanisms are not always clear. Ombrotrophication, for example, has been linked to both wet (Winkler 1988) and dry (Almquist-Jacobson and Foster 1995; Lavoie and Richard 2000) regional climates.

The paleoecological record preserved in peat deposits presents us with the opportunity to examine effects of past community change on peat accumulation. However, actual (net) organic matter accumulation is hard to infer from core profiles. Without correction for past decay, cores can only provide us with apparent rates between dated stratigraphic levels. Studies that allow for comparison of (apparent) accumulation rates between community types preserved in the same core have yielded mixed results. While some show higher rates in ombrotrophic communities (Witte and van Geel 1985; Kuhry *et al.* 1992), others have found the opposite (Kuhry *et al.* 1992; Ikonen 1995; Kuhry 1997) or show no clear pattern (Charman 1994; Lavoie and Richard 2000). This may reflect the inability of apparent rates to provide us with reliable estimates of past carbon dynamics. Alternatively, it may indicate that the effect of altered community composition depends on confounding variables such as peatland age, local physiography, and climate. In the absence of prior conceptual models of peat accumulation and decay, this dilemma cannot be resolved from the paleoecological record.

Correction for past decay requires fitting of a mathematical model to the age / depth (or cumulative mass) profile. However, the peat accumulation model that is

most commonly fitted to core data (Clymo 1984) makes several simplifying assumptions that are highly unrealistic if a site has undergone major community change. Most importantly, it assumes that mass loss in the catotelm can be described by a single decay coefficient, and that the rate of organic matter addition has been constant through time. Models that more fully represent decay or hydrological parameters affecting peat accumulation (Hilbert *et al.* 2000; Frolking *et al.* 2001) are not designed to be fitted to existing core profiles. These process-based models, however, provide important insights into the relative importance of different forcing mechanisms in controlling peat accumulation.

In spite of the fact that succession is one of the most universal and well-documented aspects of peatland development (Weber 1908; Tansley 1939; Walker 1970; Tallis 1983), existing peat accumulation models do not incorporate the concept of vegetation change. Surface water chemistry (especially pH) and water table depth are important gradients that control the composition of peatland communities (Sjörs 1950; Gignac *et al.* 1991). Sites along the rich fen - bog gradient differ not only with respect to these abiotic variables, but also in the susceptibility of their dominant vegetation to decay, with *Sphagnum* in particular being highly resistant to decomposition (Verhoeven and Toth 1995; Szumigalski and Bayley 1996b; Thormann *et al.* 1999). Representing effects of vegetation change in a peat accumulation model would therefore require not only controlling the relative abundance and productivity of different vegetation types, but also some representation of their differential decay properties. Given the limited timespan of most litter bag studies, empirical data that describe the long-term decay of specific vegetation types are mostly not available.

I here describe the development of a simulation model that examines effects of vegetation properties and environmentally driven community change on peat accumulation. The aim is not to quantitatively model the development of specific peat deposits or to predict direct effects of climate change, but rather to qualitatively examine the potential importance of vegetation properties in the carbon dynamics of peatlands. Specifically, the purpose of this work is to (a) examine the utility of a litter-

quality based approach in describing differential decay properties of peatland community types; (b) investigate the relative importance of productivity, litter quality, and abiotic factors in controlling peat accumulation over different timescales and; (c) examine the effect of sudden changes in chemical and hydrological boundary conditions on peatland carbon dynamics, and (d) determine how well changes in peat accumulation over time are reflected in final core profiles.

MODEL STRUCTURE

The model stores dry peat mass ($g \cdot m^{-2}$) in of a series of annual cohorts (Figure 4.1a). Cohort *i* is initiated in year *i* of the simulation, and receives all aboveground productivity of that year as initial mass input. In subsequent years, mass is lost through decomposition, and fresh litter may be added in the form of vascular plant roots. Mass stored within each cohort is subdivided into six litter types (aboveground herbaceous, aboveground woody, non-*Sphagnum* bryophytes, *Sphagnum*, belowground herbaceous, belowground woody), and each litter type is divided into three chemical fractions (soluble, holocellulose, and lignin; Figure 4.1b). Similar chemical characterizations of organic matter are used in studies that examine changes in carbon quality of decaying litter over time (Waksman and Stevens 1928a,b; Berg and Staaf 1980; Berg *et al.* 1984, Turetsky *et al.* 2000). The term 'lignin' is used here to refer to the portion of the organic matter that is most recalcitrant to decomposition (the acid insoluble fraction in organic matter characterization). This includes a variety of compounds other than true lignin, and the exact chemical composition of this fraction is likely to change during decomposition (Williams *et al.* 1998).

In the decay model used, the susceptibility of different organic matter fractions to decay decreases over time. Each root generation *j* added to cohort *i* in year *j* is therefore likely to decompose at a slightly different rate. In order to increase model efficiency, root inputs into each cohort are saved as annual generations only for 100 years. Roots older than 100 years are summed into 10-year root 'bins', and roots older than 1000 years are again summed and saved in 100-year bins. At the end of each year,

the total root mass remaining in annual, decadal and centennial bins after decomposition is summed and transferred to the main mass array (Figure 4.1c). Total peat depth and the stratigraphic position of each cohort are then re-calculated using assumed relationships between bulk density and overlying dry mass for different peat (litter) types (Figure 4.2).

Net primary productivity (NPP)

Aboveground NPP of four vegetation types (herbaceous, woody, bryophyte and *Sphagnum*) is predicted based on water table position and surface water pH. These can either be constant or change annually. Vegetation data (% cover values) from the Zoltai peatland dataset (ZPD; Zoltai *et al.* 2000) were summarized into the four vegetation types, yielding a total of 327 points with known water table depth, pH and vegetation cover values that are used as model input. At initialization, pH and water table depth values in these input data are re-scaled to range from zero to a user-specified maximum (S), yielding a square (S × S) lattice of environmental space recognized by the model. Yearly water table depth and pH values are re-scaled in the same manner, and percent cover of the different vegetation types is predicted by weighted averaging of data within a specified search radius of the point at which prediction is required (see Gignac *et al.* 1991). The weight given to a data point is inversely related to its distance (in lattice coordinates) from the prediction point:

$$w_p = \left[1 - \left(\frac{d_{pq}}{r}\right)^2\right]^2$$

where w_p is the weight assigned to point p; d_{pq} is the distance (in lattice coordinates) between point p and prediction point q, and r is the search radius (in lattice coordinates). If fewer than a user-specified minimum number of points are found within the search radius, the simulation is terminated.

Abundance values are converted to aboveground NPP using conversion factors for each vegetation type based on data from Szumigalski and Bayley (1996a, 1997),

Thormann and Bayley (1997a), and Thormann *et al.* (1999). These studies examined aboveground NPP of different vegetation components in a variety of peatland sites, all located between 53 ° 42' and 54 ° 41' N in east-central Alberta. Measured NPP values were matched with abundance values predicted from the ZPD for sites that occupy the same position in environmental space, and resulting abundance : NPP conversion factors (n = 3 to 7) were averaged for each vegetation type. Predicted aboveground NPP for different vegetation components is shown in Figure 4.3. Total predicted aboveground NPP (Figure 4.4a) is between 350 and 500 $g \cdot m^{-2} \cdot yr^{-1}$ for most of the environmental space recognized by the model. This is slightly higher than measured values from continental western Canada (Szumigalski and Bayley 1996a; Thormann and Bayley 1997a).

Total NPP (NPP_{total}; Figure 4.4b) is calculated from aboveground NPP by assuming fixed aboveground:belowground ratios for woody and herbaceous vegetation. Belowground NPP is notoriously hard to quantify, particularly in peatlands where living roots and rhizomes are embedded in an organic matrix (Saarinen 1996). While many early studies assumed an above:belowground ratio of 1:1 (see Bradbury and Grace 1983), recent work using ^{14}C labelling suggests that fine roots alone can account for 75% of annual NPP in some *Carex* species (Saarinen 1996). Several studies have found over 90% of total living biomass for some taxa to be below ground (Wallén 1986; Sjörs 1991; Saarinen 1996). Values presented in Figure 4.4b assume above:belowground NPP ratios of 3:2 for woody and 1:3 for herbaceous taxa. Because of the high assumed belowground contribution for herbaceous taxa, total NPP values predicted by the model are high. In herb-dominated environments, total NPP exceeds 1000 $g \cdot m^{-2} \cdot yr^{-1}$, which resembles published estimates for marshes rather than fens (Campbell *et al.* 2000).

Living biomass is generally concentrated in the upper 15 - 20 cm of the peat column (Dennis and Johnson 1970; Bernard and Fiala 1986). Exact vertical distributions of belowground biomass vary between taxa (Miller *et al.* 1982; Wallén 1986; Bernard and Fiala 1986; Sjörs 1991), and only plants with aerenchymatous roots

have a significant portion of their roots below the water table. Saarinen (1996) found live *Carex* roots at over 200 cm depth. The model assumes an exponential decline in herbaceous root inputs with depth, with roots penetrating to a maximum depth of 200 cm, but eighty percent of all inputs occurring within the upper 20 cm of peat (Figure 4.5a). Woody roots are assumed to be evenly distributed above the water table, or within the upper 10 cm of peat if the water table is within 10 cm of the surface (Figure 4.5b).

Decay

The model uses a combination of external (temperature, oxygen availability and pH) and internal (nitrogen and lignin-related) decay modifiers that act upon user-specified surface turnover rates for the different chemical fractions (Figure 4.6). Turnover rates (α) describe the proportion of mass (M) present at the beginning of a given year *i* that is lost due to decay during that year, i.e.

$$M_{i+1} = M_i \times (1-\alpha)$$

If α remains constant through time, this represents exponential decay. However, both external and internal decay modifiers gradually decrease turnover rates. Internal decay modifiers depend on litter type and are affected by the initial chemical composition of the litter and its previous decay history. External decay modifiers affect all fractions equally and are dependent on environmental boundary conditions and the stratigraphic position of a cohort.

Internal decay modifiers

Relationships between litter chemistry and decay have been discussed extensively in the literature, and there is no general agreement on which aspect of litter quality best predicts susceptibility to decay. Lignin content, total N, C:N ratios and lignin:N ratios have all been related successfully to observed differences in decay rates (e.g. Bartsch and Moore 1985; Taylor and Parsons 1989; Aerts and de Caluwe 1997; Bridgham *et al.* 1998; Thormann *et al.* 2001). The decay model used here is largely

based on work by Björn Berg and co-workers (Berg and Staaf 1980; Berg *et al.* 1982, 1984; Berg 1986; Berg and Ekbohm 1991), who studied decay of different litter types and associated changes in carbon quality in forest ecosystems over up to five years. Their data suggest that nitrogen availability positively affects decay of the soluble (SOL) and holocellulose (HOL) fractions in the early stages of decomposition. Lignin (LIG) decay is not affected by nitrogen availability, and lignin mass generally does not decrease in early stages of decay. During later stages of decomposition, lignin-related variables become increasingly important in controlling decay rates.

Lignin and lignin-like compounds are often associated with cellulose, and the decay of part of the holocellulose fraction is tightly linked to that of lignin. Berg *et al.* (1984) followed changes in lignocellulose quotient (Q = HOL / (HOL + LIG)) over time and generally observed rapid decreases during early stages of decay. However, Q eventually approached a constant value, indicating that the remaining holocellulose decayed at the same rate as lignin. Berg *et al.* (1984) determined the point at which this occurred by fitting asymptotic negative-exponential models to changes in Q as a function of remaining lignocellulose. Asymptotic values of Q (here referred to as Q_c) differed between litters and varied from 0.40 to 0.69. The model allows for specification of a litter-specific Q_c value.

Nitrogen content

Surface turnover rates for the soluble and holocellulose fractions in each litter type are adjusted at initialization based on N content and a user-specified Nitrogen factor (θ). The N contents assumed for different litter / peat types are based on average values measured for peat samples from continental western Canada (Table 1). No adjustment is made for the most N-rich litter type (herbaceous). N-adjusted turnover rates for SOL and HOL in the litter with lowest N-content (*Sphagnum*) are calculated as e.g.

$$\alpha_{Nc,SOL} = \frac{\alpha_{Sf,SOL}}{\theta}$$

where $\alpha_{Sf,SOL}$ is the user-specified surface turnover rate for the soluble fraction. The nitrogen factor therefore specifies the difference in surface turnover rates between the litter types with the highest and lowest nitrogen content. Adjusted turnover rates for woody and bryophyte remains are calculated based on their assumed nitrogen content using linear interpolation between these maximum and minimum N-adjusted rates.

Lignin-related variables

Lignin turnover rates are not affected by N content; they are the same for all litter types. The decomposability of lignin in the model declines as lignin mass decreases, reflecting increased recalcitrance of the remaining material. Each year, the turnover rate for lignin in each cohort (or root generation within each cohort) is calculated as

$$\alpha_{i,LIG} = \left(\frac{M_{i,LIG}}{M_{0,LIG}}\right) \times \alpha_{Sf,LIG}$$

where $M_{i,LIG}$ is lignin mass at the beginning of year i, $M_{0,LIG}$ is the original lignin mass at the time the cohort / root generation is initiated, $\alpha_{i,LIG}$ is the lignin turnover rate in year i, and $\alpha_{Sf,LIG}$ is the maximum (surface) lignin turnover rate. Thus, lignin turnover follows the 'linear' decay rule of Clymo *et al.* (1998), where mass loss depends on the proportion of original mass that remains at the beginning of a given year.

Turnover rates for the other chemical fractions gradually approach that of lignin, with rates for each litter in year i depending on its lignocellulose quotient, i.e.

$$\alpha_{Lq,i,k,HOL} = \alpha_{i,LIG} + \left(Q_{i,k} - Q_{c,k}\right) \times \left(\frac{\alpha_{Nc,k,HOL} - \alpha_{i,LIG}}{Q_0 - Q_{c,k}}\right) \qquad \text{if } Q_{i,k} > Q_{c,k}\text{; else}$$

$$\alpha_{Lq,i,k,HOL} = \alpha_{i,LIG}$$

where $\alpha_{Lq,i,k,HOL}$ is the litter quality dependent turnover rate for holocellulose in year i in litter k; $Q_{i,k}$ is the lignocellulose quotient of litter k at the beginning of year i; $Q_{c,k}$ is the (user-specified) value of Q at which holocellulose in litter k decays at the same rate

as lignin; $\alpha_{Nc,k,HOL}$ is the N-adjusted holocellulose turnover rate of litter k; $\alpha_{i,LIG}$ is the turnover rate for lignin in year i; and Q_0 is the lignocellulose quotient of fresh, easily decomposable litter (assumed to be 0.715, based on initial HOL and LIG contents of 50 and 20 percent, respectively).

External decay modifiers

Decreasing temperature with depth, anoxia in the permanently waterlogged catotelm, and the low pH of some peatland types all decrease the rates of litter turnover. Each of these factors is represented as a multiplier that varies in magnitude between zero and one. In a given year,

$$\alpha_{Ac,coh,k,f} = \alpha_{Lq,coh,k,f} \times Zt_{coh} \times Zoa_{coh}$$

where $\alpha_{Ac,coh,k,f}$ is the actual (final) turnover rate for chemical fraction f in litter k in cohort *coh*; $\alpha_{Lq,,coh,k,f}$ is the litter-quality dependent turnover rate for fraction f in litter k in cohort *coh*; Zt_{coh} is a cohort (depth) dependent temperature modifier, and Zoa_{coh} is a pH-dependent oxic:anoxic modifer that depends on both cohort depth and the current water table position. The temperature modifier (Figure 4.7) is similar in shape to that used by Frolking *et al.* (2001) in their peat decomposition model (PDM). Sensitivity analysis of PDM suggests that effects of temperature change with depth on peat accumulation are minor compared to those of other variables. No attempt was made here to fine-tune the shape of the temperature modifier.

pH and oxygen availability

Rates of organic matter turnover in the permanently waterlogged catotelm are at least an order of magnitude lower than those in the acrotelm (Clymo 1984). However, effects of external decay modifiers are impossible to infer directly from natural peat deposits, as changes in oxygen availability and temperature with depth are accompanied by marked changes in organic matter quality, and observed differences in decay rates reflect the combined effects of these variables. Laboratory incubations clearly indicate that a given material decomposes more quickly under aerobic than

under anaerobic conditions (Magnusson 1993; Updegraff *et al.* 1995; Bridgham *et al.* 1998; Bergman *et al.* 1999; Scanlon and Moore 2000). Oxic:anoxic ratios for rates of CO_2 and CH_4 production vary with material type and length of the incubation period, with reported values ranging from ~2:1 to more than 30:1 (see Scanlon and Moore 2000).

Studies that have examined the effect of pH on rates of C mineralization are less conclusive. Direct effects of pH are hard to observe, because use of native vegetation generally involves systematic differences in the chemical quality of litters from different peatland types. Experiments using standard litters and incubation studies suggest that C mineralization may be slower in acidic environments (e.g. Verhoeven *et al.* 1990; Bergman *et al.* 1999), although several recent studies (Szumigalski and Bayley 1996b; Bridgham *et al.* 1998) have found no such effect. Bridgham *et al.* (1998) found that CH_4 production was inhibited in ombrotrophic situations, although total C mineralization was similar to that in peat from minerotrophic sites. In PDM, Frolking *et al.* (2001) assumed oxic:anoxic decay ratios of 10:1 for fens and 40:1 for bogs based on greater hydrologic isolation and higher acidity of catotelm peat in bogs.

The model described here allows pH-dependent differences in both aerobic and anaerobic turnover rates. Transition from oxic conditions at the surface to fully anoxic conditions in the catotelm is assumed to be gradual, and the position of each cohort on this gradient depends on the proportion of time (yr^{-1}) it spends above the water table. Temporal fluctuations around the mean annual water table position (ω) are assumed to be normally distributed, with greater amplitude (ϕ) if the water table is close to the peat surface (Figure 4.8a). The proportion of each year that a cohort spends above the water table (β_{coh}) is predicted from its stratigraphic position and the cumulative distribution function of a normal distribution with mean = ω and 2SD = ϕ / 2 (Figure 4.8b). The value of the oxic:anoxic decay modifier is then calculated as

$$Zoa_{coh} = \beta_{coh} \times Zo_{coh} + (1 - \beta_{coh}) \times Za_{coh}$$

where Zo_{coh} is the value of the decay modifier under fully oxic conditions, and Za_{coh} is the value of the decay modifier under fully anoxic conditions. At initialization, the model calculates slopes and intercepts of linear equations that describe changes in Zo and Za with pH from user-specified decay multipliers (π_1 and π_2) and anoxic:oxic ratios (ρ_1 and ρ_2) at two reference pH levels. Zo_{coh} and Za_{coh} are then calculated annually from these equations and the pH of water surrounding the cohort. For simplicity, this is assumed to equal the surface water pH at the time the cohort was initiated

TESTING MODEL BEHAVIOUR

Sensitivity analysis

In order to examine the relative importance of parameters related to litter quality, NPP and decay in controlling rates of organic matter accumulation, a simplified version of the model was subjected to a sensitivity analysis. The parameters manipulated are summarized in Table 4.2. The simplified model only recognized one vegetation type that produced both above- and belowground litters. The herbaceous root function (Figure 4.5 a) was used to predict the vertical distribution of root inputs. Water table depth and pH remained fixed throughout each simulation. Individual parameter values were increased or decreased by 25% relative to a base-line scenario, with the direction of adjustment aimed at increasing organic matter accumulation relative to the base-line case. Because there was only one vegetation type, nitrogen-moderated turnover rates ($\alpha_{Nc,SOL}$, $\alpha_{Nc,HOL}$) were specified directly. Aboveground NPP and parameter values for the oxic:anoxic decay modifier (ρ and π) were also specified directly and remained fixed throughout each simulation.

Static peatland types

A series of simulations examined differences in organic matter accumulation between peatland types over 8,000 years. NPP and decay-related parameters were calculated as described for the full model above; pH and water table depth were held

constant for each simulation. Peatlands examined were rich fens (pH 6.5), transitional fens (pH 5.5) and bogs / poor fens (pH 4.5). Organic matter accumulation in each of these types was examined at three water table depths: wet (5 cm); medium (25 cm) and dry (45 cm). The basic parameterization (Table 4.3) was the same for all simulations. Differences in total and litter-specific NPP values and oxic:anoxic decay parameters thus reflect environmental differences between the sites. Initial organic matter quality (SOL, HOL and LIG content) was the same for all vascular litter types; in bryophytes and *Sphagnum* it was dependent on water table depth, with higher lignin content (up to 29%) in dry sites. This reflects well-documented differences in the susceptibility of hummock and hollow taxa to decay (Rochefort *et al.* 1990; Johnson and Damman 1991, 1993) that may be related to initial organic matter quality (Pakarinen and Vitt 1974; Turetsky 2002).

Effects of community change

In order to examine effects of community change on peat accumulation, a series of simulations was run over 6000 years. The basic model parameterization was the same as that used for static simulations (Table 4.3). Each run was initiated with a pH of 6 and ω = 10 cm, which resembles initial environmental conditions reconstructed by Kuhry *et al.* (1993) for several peat deposits in continental western Canada. Between 2800 and 3000 years, pH and water table depth were gradually adjusted to a new set of target conditions. Water table depth either remained constant or increased to 20, 30 or 40 cm below the peat surface. At the same time, pH either remained constant or decreased to 4.5, representing succession from rich fen to poor fen or bog.

Inferred organic matter accumulation

Apparent and decay-corrected rates of mass accumulation were calculated from final core profiles of non-static simulations in order to assess our ability to infer past accumulation rates in sites that have experienced marked community change.

Apparent rates are calculated from the final peat mass between stratigraphic levels of known age, i.e.

$$\frac{\Delta M}{\Delta T} = \frac{(M_2 - M_1)}{(T_2 - T_1)}$$

where $\Delta M/\Delta t$ is the change in peat mass during time interval T; M_1 and M_2 represent total peat mass below reference levels 1 and 2, respectively, and T_1 and T_2 are the years in which peat at the two reference levels was first produced.

Decay-corrected rates were calculated by fitting 'Clymo-type' curves to final cumulative mass / age profiles. For the case in which annual turnover rates are dependent on the fraction of original material remaining,

$$M_T = \frac{p}{\alpha} \times \ln(1 + \alpha T)$$

where M_T is total peat mass above the level corresponding to time T, p is the rate of mass input, and α is the annual turnover rate (Clymo *et al.* 1998). Once p and α are known, net (decay-corrected) rates of organic matter accumulation can be calculated as

$$\frac{\Delta M}{\Delta T} = \frac{p}{(1 + \alpha T)}$$

(Clymo *et al.* 1998). All rates were calculated as yearly averages over 500-year periods.

RESULTS

Sensitivity analysis

The baseline scenario used in sensitivity analysis accumulated 300 $kg \cdot m^{-2}$ of peat over 10,000 years. Parameter adjustments produced increases in final accumulated mass between 3 and more than 60 % (Figure 4.9). Total NPP had the strongest effect on accumulation over the first 50 years. It was then replaced by Q_c, which remained the most important parameter up until 10,000 years (Table 4.4).

The relative importance of individual parameters changed through time, with three main patterns apparent from the data (Table 4.4): The effect of N-dependent decreases in surface turnover rates (α_{Nc}) was most pronounced (10% increase in accumulated mass) within the first 10 years. By 5000 years this had declined to 3%. Total NPP and two of the three lignin-related parameters (original LIG content and Q_c) were important throughout, but their effect peaked between 500 and 1000 years. Water table depth showed a similar pattern, although its effect was small for the first 100 years. A third group of parameters ($\alpha_{Sf,LIG}$, ρ and π) had no or steadily increasing effects on accumulated mass during the first 1000 years. Their effect then remained constant ($\alpha_{Sf,LIG}$, π) or continued to increase (ρ) up to 10,000 yrs.

Static peatland types

In simulations with constant pH and water table depth, total annual NPP ranged from 621 to 1076 $g \cdot m^{-2} \cdot yr^{-1}$ (Table 4.5). The rich and transitional fens were similar in total productivity and more productive than the bogs / poor fens. Herbaceous NPP accounted for a third or more of total productivity in all cases except the dry bog / poor fen. It was highest (~80%) in wet transitional and rich fens. The contribution of woody vegetation to total NPP increased from wet to dry environments and was highest in the bog / poor fen scenario at all water table depths. Non-*Sphagnum* bryophytes contributed comparatively little to total NPP (<10% in all cases), and *Sphagnum* was most important (29-33% of total NPP) at low pH. However, *Sphagnum* still contributed 11-23% of total productivity in rich and transitional fens except under the wettest conditions.

Surface turnover rates for fresh litter shown in Table 4.5 reflect the combined effect of litter quality and external decay modifiers, i.e. they represent total mass loss expected from litter bags during the first year of decay. Values range from 10% turnover for *Sphagnum* in the dry bog / poor fen scenario to 43% mass loss from herbaceous litter in dry and medium rich fens. Total mass accumulation over 8000 years was highest in the wet poor fen / bog (568 $kg \cdot m^{-2}$) and lowest in the dry rich fen

(100 $kg \cdot m^{-2}$; Figure 4.10). Rich fens had the lowest organic matter accumulation within each water table class over 8000 years. At high and medium water tables, bogs / poor fens accumulated most peat, whereas transitional fen accumulated most within the lowest water table class. In several cases, the relative peat accumulation potential of different community types changed over time. During the first 3000 years, for example, rich fens at medium water tables accumulated more peat than bogs / poor fens (Figure 4:10).

Effects of community change

Changes in environmental boundary conditions and consequent community succession had marked impacts on organic matter accumulation. Transition from rich fen to poor fen / bog led to increased organic matter accumulation relative to the base-line scenario only if water levels remained constant (Figure 4.11a). Lowered water tables resulted in a net loss of organic matter for 350 - 2500 years, depending on the type of community established. Bogs / poor fens (Figure 4.11a) recovered faster and showed higher net rates of mass accumulation at the end of the simulation period than rich fens with similar water table depths (Figure 4.11b). Shapes of cumulative mass / age profiles from the same set of simulations (Figure 4.11 c and d) range from markedly concave (final pH = 4.5; ω = 10 cm) to flat (final pH = 4.5; ω = 40 cm) and convex (final pH = 6; ω = 40 cm).

Inferred organic matter accumulation

Clymo-type accumulation models fit the 'concave' profiles in Figure 4.11c well, with an near-perfect fit for the baseline case (Table 4.6). Consequently, inferred net (decay-corrected) rates of organic matter accumulation for the baseline scenario closely match actual rates (Figure 4.12b). Apparent rates strongly underestimate net organic matter accumulation during the first half of the simulation period, and overestimate during the second half (Figure 4.12a).

In dynamic simulations, neither of the core-based methods provided accurate estimates of net accumulation in the past. Decay-corrected rates were generally closer

to true values than apparent rates, but absolute errors for individual 500-year periods were as high as 100 $g \cdot m^{-2} \cdot yr^{-1}$ (Figure 4.12b). If net organic matter accumulation increased in recent times, decay-corrected rates overestimate actual rates during early phases of peat accumulation and underestimate recent rates. In cases where lowered water tables decreased recent accumulation compared to the baseline case, decay-corrected rates strongly underestimate initial accumulation rates.

DISCUSSION

The results have several important implications, both in terms of predicting peatland response to environmental change and the use of paleoecological data in inferring past peatland carbon dynamics. Total peat accumulation in static simulations generally falls within the range of values reported in the literature, except for the dry scenarios that are unlikely to persist over extended periods of time. Nevertheless, specific assumptions and parameter values used are open to debate. The decay model chosen is complex and requires specification of several parameters that have never been quantified in a peatland context. For example, initial organic matter quality and the degree of association between lignin and cellulose (Q_c in the model) are unknown quantities for most taxa, yet sensitivity analysis identifies them as key parameters in long-term peat accumulation. Thus, while initial turnover rates for different vegetation types (Table 4.5) are similar to values measured by litter bag studies in continental western Canada (Szumigalski and Bayley 1996b; Thormann and Bayley 1997b), few data are available to assess how accurately the model describes the long-term decay properties of different vegetation types.

In spite of these uncertainties, the litter-quality based approach has a number of desirable properties. Most importantly, it describes differences in the short- and long-term decomposability of different vegetation types using parameters that can be measured over reasonable timescales. Berg *et al.* (1984) determined Q_c values of different litter types after 2-5 years of *in situ* decomposition. Whether the 'functional groups' chosen here are appropriate for describing differences in the susceptibility of

peatland community types to decay remains to be seen. For bryophytes, organic matter quality may depend on the position of taxa along the hummock-hollow gradient (Pakarinen and Vitt 1974; Turetsky 2002). This is easily incorporated into the present model structure. Differences in organic matter quality that do not correlate with habitat parameters recognized by the model would require inclusion of additional litter types and modelling of above- and belowground productivity for these litters.

The use of empirical response surfaces to model aboveground productivity seems promising. The approach captures habitat-dependent changes in the abundance of major groups (Figure 4.3) without assuming specific response models for individual taxa or the group as a whole. This is important because several of the groups do not display a unified response in the environmental parameter space recognized by the model. The non-*Sphagnum* bryophyte category, for example, includes brown mosses characteristic of wet rich fens as well as feather mosses that grow on dry hummocks in a variety of peatland types. The response surface approach accounts for this variability without requiring detailed information about the habitat requirements of specific taxa. Several detailed datasets that describe peatland community composition exist for continental western Canada (Zoltai *et al.* 2000; Gignac *et al.* 2000), and these could potentially provide abundance data for any variety of vegetation classes.

Abundance : NPP conversion factors and aboveground : belowground NPP ratios for vascular taxa require further calibration. Comparison with existing data suggests that herbaceous NPP values predicted by the model are probably too high; bryophyte NPP values too low (Campbell *et al.* 2000). In the parameterization used here, the high herbaceous inputs are balanced by high (both initial and long-term) decomposability of herbaceous litters. Further data are needed to test the validity of this particular aspect of the model's behaviour. Belowground NPP values for different functional groups probably represent the most important gap in our current knowledge.

Model sensitivity and static peatland types

Sensitivity analysis identified litter quality, especially lignin-related variables, as critical in determining long-term peat accumulation dynamics. While this was expected, it has to be stressed that all parameter adjustments made during sensitivity analysis were by the same proportional amount, which is likely to be high for some variables and low for others. Natural differences in water table depth between peatland communities are far greater than the 5 cm change modelled, (e.g. Zoltai *et al.* 2000), and paleoecological data indicate that 10- to 15 cm changes can occur rapidly at a given site (Kuhry *et al.* 1993). Therefore, the results of sensitivity analysis may not reflect the true ecological importance of individual parameters. Furthermore, the complexity of the decay model used precluded testing of the many likely interactions between variables, and exact results would probably be different for altered baseline conditions.

Nevertheless, some important patterns emerge. Most notably, the relative importance of different parameters in controlling rates of peat accumulation changes over time. Nitrogen content, generally regarded as one of the most important predictors of organic matter turnover (Hunt 1977; Taylor and Parsons 1989; Szumigalski and Bayley 1996b; Scheffer and Aerts 2000), has a significant effect only for the first 10 years. This implies that the results of short-term decomposition studies have limited value in predicting long-term organic matter dynamics in peatlands. Several studies have observed a switch from nitrogen to lignin as the most important factor in controlling long-term decay dynamics (Berg and Staaf 1980; Taylor and Parsons 1989), and long-term litter bag studies demonstrate that trends observed after a few years may not be maintained over longer timescales (Latter *et al.* 1998).

Parameters that reach their maximum importance after 500-1000 years (NPP, original LIG content and Q_c; Table 4.4) all affect how much mass is transferred to the catotelm, either by increasing total mass input, or by decreasing acrotelm turnover rates. Their subsequent decline in importance indicates that these initial differences are partially compensated for by mass loss in the catotelm. For example, a high value of

Q_c, (i.e. a high proportion of cellulose is tightly bound to lignin) allows a greater proportion of the original cellulose to reach the catotelm. However, once Q_c is reached, lignin controls mass loss of both lignin and cellulose, with higher mass loss in litters that still contain a significant portion of cellulose. No such compensation is apparent for the original lignin turnover rate ($\alpha_{Sf,LIG}$) and parameters involved in the oxic:anoxic decay modifier (ρ and π). Lignin turnover rates are a function of previous lignin turnover, which is controlled by external decay modifiers. Since external decay modifiers affect all chemical fractions equally, their effect does not depend on the quality of the remaining material.

Temporal changes in the importance of the different input parameters detected during sensitivity analysis are mirrored in the peat accumulation dynamics of static peatland types. Initial organic matter accumulation in fens, for example, is similar to that in bogs, because the high productivity of fens compensates for their faster litter turnover rates. Over longer timescales, however, lower organic matter quality and anoxic:oxic decay ratios lead to greater peat accumulation in bogs.

The combined effect of litter quality and anoxic:oxic ratios is most apparent in the large difference in final accumulated mass between wet peatland types (Figure 4.10a), because high water levels allow a greater proportion of material to reach the catotelm. In bogs, the relative quality of this material is lower, and it is further protected from decay by lower anoxic:oxic ratios. At intermediate and low water levels, differences between sites are less pronounced because easily decomposable litter is largely lost before it reaches the catotelm. Furthermore, differences in initial litter quality are less marked, because *Sphagnum* makes up a significant proportion of NPP at all pH levels modelled.

While many of these specific results reflect assumptions inherent in the design of the model, they point towards strong litter quality-dependent controls over organic matter accumulation. They further indicate that factors controlling peat accumulation differ in relative importance between site types and are not constant over time. When comparing peat accumulation potential of different vegetation types, the timescale of

reference should therefore be made clear. Furthermore, data used for predictive purposes should be matched with the timescale over which prediction is required.

Effects of environmental change

In dynamic simulations, lowered peatland water tables result in a net loss of organic matter for several centuries, irrespective of the type of community established. The sudden changes in parameter values imposed on the model resemble patterns observed in the paleoecological record (Kuhry *et al.* 1993). However, changes in water table depth that occur during peatland succession are not necessarily a good analogue for effects of climate change. In models of autogenic peatland succession (Weber 1908), lowered water levels are generally attributed to increased elevation of vegetation over a (static) water table, not a net decrease in the amount of water stored in peat. This distinction is important, because the negative mass balances modelled here largely result from the decay of easily decomposable material that is transferred from the catotelm back into the acrotelm.

The results obtained are extreme for a number of reasons. Most importantly, water table position was specified relative to the peat surface rather than in terms of storage. Material transferred from the catotelm to the acrotelm decayed fast and had to be replaced by transfer of more material from the catotelm until the new (deep) acrotelm attained a stable state. This usually did not occur until water storage had decreased by substantially more than implied by the original decline in water level. Furthermore, the initial wet rich fen was probably more sensitive to changed water levels than many other community types because of the high decomposability of its (largely herbaceous) litter.

While the magnitude of simulated mass loss is probably unrealistic, negative carbon balances during periods of drought have been observed in several studies (Waddington and Roulet 1996; Alm *et al.* 1999; Joiner *et al.* 1999), indicating that many peatlands are likely to become net carbon sources as a result of climate change.

Results obtained here suggest that the magnitude and duration of this effect will depend not only on the severity of change, but also on initial community composition (which determines litter quality), and the peat accumulation potential of newly established communities. Irrespective of the timescale of interest, water table stability will be the most critical factor determining peatland response to climatic change. Unfortunately, we presently have little quantitative information about the sensitivity of water tables in different peatland types to altered climatic boundary conditions.

Limitations of paleoecological data

Whether or not modelled changes in peat accumulation following environmental change are realistic, simulated core profiles (Figure 4.11c and d) point towards several important limitations in the use of paleoecological data to reconstruct past peatland dynamics. Apparent accumulation rates calculated from peat cores are systematically biased; they underestimate net organic matter accumulation in older core sections and overestimate recent rates. This is inevitable if organic matter produced at the surface undergoes gradual decay over time (Clymo 1984) and has several important implications that have been discussed extensively in the past (Tolonen *et al.* 1992; Korhola *et al.* 1995; Clymo *et al.* 1998).

Fitting of 'Clymo-type' accumulation models to cumulative mass / age profiles successfully eliminates this bias if the basic assumptions of these models are met. This is the case for the baseline scenario in which pH and water table depth remain constant through time. In spite of the complicated decay model used here, the 'linear' decay rule of Clymo *et al.* (1998) describes the simulated profile almost perfectly, because long-term mass accumulation is controlled by lignin decay, which follows the linear model.

In simulations that involve community change, several basic assumptions of the Clymo model are violated, and inferred 'decay-corrected' rates are systematically biased (Figure 4.12b). Thus, while the fitting of simple models to core profiles allows for broad comparisons between long-term peat accumulation in different peatland

types or regions, (Tolonen *et al.* 1992; Korhola *et al.* 1995; Tolonen and Turunen 1996; Clymo *et al.* 1998), it is potentially misleading when examining temporal changes in the organic matter dynamics of individual cores. Moreover, the excellent fit of such models to simulated profiles (Table 4.6) indicates that departure from their assumptions is not necessarily apparent from the cumulative mass / age profile preserved.

The ubiquity of community change apparent in macrofossil records (Walker 1970; Tallis 1983), measured and modelled differences in peat accumulation potential between community types (Tolonen and Turunen 1996; Thormann *et al.* 1999; Robinson and Moore 1999; Frolking *et al.* 2001), and diverse cumulative mass / age relationships in core profiles (Clymo *et al.* 1998; Yu *et al.* 2000) all suggest that organic matter dynamics of peatlands have responded flexibly to environmental change in the past. However, results obtained here indicate that such changes are not necessarily apparent from dated core profiles. Most notably, neither of the methods tested can detect past periods of negative mass balance. This implies that periods of net organic matter loss from peatlands may have occurred repeatedly in the past, but are impossible to detect by current methods of paleoecological interpretation.

The paleoecological record itself may hold the key to overcoming this apparent limitation. In many cases, macrofossil evidence preserved in peat allows for quantitative reconstruction of past environmental conditions (e.g., Janssens *et al.* 1992; Kuhry *et al.* 1993; Chapter 2), i.e., peat deposits conserve a record of temporal changes in the environment under which they were formed. Inferred environmental data represent boundary conditions that can be used as input to dynamic models, and simulated profiles can be validated by comparison to actual stratigraphies. Current process models cannot quantitatively predict organic matter accumulation in peatlands within a changing environmental framework over decadal or centennial timescales. A more dynamic approach to the interpretation of paleoecological records would greatly increase their utility in validating model output and in predicting future responses of peatlands to environmental change

LITERATURE CITED

Aerts R and de Caluwe H. 1997. Nutritional and plant-mediated controls on leaf litter decomposition of *Carex* species. *Ecology* 78:244-260.

Alm J, Schulman L, Walden J, Nykänen H, Martikainen PJ and Silvola J. 1999. Carbon balance of a boreal bog during a year with an exceptionally dry summer. *Ecology* 80:161-174.

Alm J, Talanov A, Saarnio S, Silvola J, Ikkonen E, Aaltonen H, Nykänen H and Martikainen PJ. 1997. Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. *Oecologia* 110:423-431.

Almquist-Jacobson H and Foster DR. 1995. Toward an integrated model for raised-bog development: Theory and field evidence. *Ecology* 76:2503-2516.

Bartsch I and Moore TR. 1985. A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Québec. *Canadian Journal of Botany* 63:1241-1248.

Berg B. 1986. Nutrient release from litter and humus in coniferous forest soils - a mini review. *Scandinavian Journal of Forest Research* 1:359-369.

Berg B and Ekbohm G. 1991. Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest. *Canadian Journal of Botany* 69:1449-1456.

Berg B, Ekbohm G and McClaugherty C. 1984. Lignin and holocellulose relations during long-term decomposition of some forest litters. Long-term decomposition in a Scots pine forest. IV. *Canadian Journal of Botany* 62:2540-2550.

Berg B, Hannus K, Popoff T and Theander O. 1982. Changes in organic chemical components of needle litter during decomposition. Long-term decomposition in a

Scots pine forest. I. *Canadian Journal of Botany* 60:1310-1319.

Berg B and Staaf H. 1980. Decomposition rate and chemical changes of Scots Pine needle litter. II Influence of chemical composition. *Ecological Bulletin* (Stockholm) 32:373-390.

Bergman I, Lundberg P and Nilsson M. 1999. Microbial carbon mineralization in an acid surface peat: effects of environmental factors in laboratory incubations. *Soil Biology and Biochemistry* 31:1867-1877.

Bernard JM and Fiala K. 1986. Distribution and standing crop of living and dead roots in three wetland *Carex* species. *Bulletin of the Torrey Botanical Club* 113:1-5.

Bradbury IK and Grace J. 1983. Primary production in wetlands. Pages 285-310 in: Gore AJP. editor. *Mires: swamp, bog, fen and moor: General studies*. Ecosystems of the World 4A, Elsevier Scientific Publishing Company. Amsterdam.

Bridgham SD, Updegraff K and Pastor J. 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. *Ecology* 79:1545-1561.

Camill P. 1999. Peat accumulation and succession following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Ecoscience* 6:592-602.

Campbell C, Vitt DH, Halsey LA, Campbell IK, Thormann MN and Bayley SE. 2000. Net primary production and standing biomass in northern continental wetlands. Information Report NOR-X-369, Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre. Edmonton, Alberta.

Charman DJ. 1994. Patterned fen development in northern Scotland: developing a hypothesis from palaeoecological data. *Journal of Quaternary Science* 9:285-297.

Clymo RS. 1984. The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London* B 303:605-654.

Clymo RS, Turunen J and Tolonen K. 1998. Carbon accumulation in peatland. *Oikos* 81:368-388.

Dennis JG and Johnson PL. 1970. Shoot and rhizome-root standing crops of tundra vegetation at Barrow, Alaska. *Arctic and Alpine Research* 2:253-266.

Frolking S, Roulet NT, Moore TR, Richard PJH, Lavoie M and Muller SD. 2001. Modeling northern peatland decomposition and peat accumulation. *Ecosystems* 4:479-498.

Gignac LD, Halsey LA and Vitt DH. 2000. A bioclimatic model for the distribution of *Sphagnum*-dominated peatlands in North America under present climatic conditions. *Journal of Biogeography* 27:1139-1151.

Gignac LD, Vitt DH and Bayley SE. 1991. Bryophyte response surfaces along ecological and climatic gradients. *Vegetatio* 93:29-45.

Gignac LD, Nicholson BJ and Bayley SE. 1998. The utilization of bryophytes in bioclimatic modeling: predicted northward migration of peatlands in the Mackenzie River Basin, Canada, as a result of Global Warming. *The Bryologist* 101:572-587.

Gignac LD and Vitt DH. 1994. Responses of northern peatlands to climate change: Effects on bryophytes. *Journal of the Hattori Botanical Laboratory* 75:119-132.

Gignac LD, Vitt DH, Zoltai SC and Bayley SE. 1991. Bryophyte response surfaces along climatic, chemical, and physical gradients in peatlands of western Canada. *Nova Hedwigia* 53:27-71.

Gorham E. 1991. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* 1:182-195.

Gunnarsson U, Rydin H and Sjörs H. 2000. Diversity and pH changes after 50 years on the boreal mire Skattlösbergs Stormosse, Central Sweden. *Journal of Vegetation Science* 11:277-286.

Halsey LA, Vitt DH and Bauer IE. 1998. Peatland initiation during the Holocene in Continental Western Canada. *Climatic Change* 40:315-342.

Halsey LA, Vitt DH and Gignac LD. 2000. *Sphagnum*-dominated peatlands in North America since the Last Glacial Maximum: Their Occurrence and Extent. *The Bryologist* 103:334-352.

Hilbert DW, Roulet N and Moore T. 2000. Modelling and analysis of peatlands as dynamical systems. *Journal of Ecology* 88:230-242.

Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ and Xiaosu D. 2001. *Climate Change 2001: The Scientific Basis*. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge.

Hunt HW. 1977. A simulation model for decomposition in grasslands. *Ecology* 58:469-484.

Ikonen L. 1995. Rate of carbon accumulation in a raised bog, southwestern Finland *Geological Survey of Finland Special Paper* 20:135-137.

Janssens JA, Hansen BCS, Glaser PH and Whitlock C. 1992. Development of a raised-bog complex. Pages 189-221 in: Wright HE Jr, Coffin BA and Aaseng NE. (editors). *The patterned peatlands of Minnesota*. University of Minnesota Press. Minneapolis.

Johnson LC and Damman AWH. 1991. Species-controlled *Sphagnum* decay on a South Swedish raised bog. *Oikos* 61:234-242.

Johnson L and Damman AWH. 1993. Decay and its regulation in *Sphagnum* peatlands *Advances in Bryology* 5:249-296.

Joiner DW, Lafleur PM, McCaughey JH and Bartlett PA. 1999. Interannual variability in carbon dioxide exchanges in a boreal wetland in the BOREAS northern study

area. *Journal of Geophysical Research* 104:27663-27672.

Kolchugina TP and Vinson TS. 1993. Carbon balance of the continuous permafrost zone of Russia. *Climate Research* 3:13-21.

Korhola A, Tolonen K, Turunen J and Jungner H. 1995. Estimating long-term carbon accumulation rates in boreal peatlands by radiocarbon dating. *Radiocarbon* 37:575-584.

Kuhry P. 1994. The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. *Journal of Ecology* 82:899-910.

Kuhry P. 1997. The palaeoecology of a treed bog in western boreal Canada: a study based on microfossils, macrofossils and physio-chemical properties. *Review of Palaeobotany and Palynology* 96:183-224.

Kuhry P, Halsey LA, Bayley SE and Vitt DH. 1992. Peatland development in relation to Holocene climate changes in Manitoba and Saskatchewan (Canada). *Canadian Journal of Earth Sciences* 29:1070-1090.

Kuhry P, Nicholson BJ, Gignac LD, Vitt DH and Bayley SE. 1993. Development of *Sphagnum* dominated peatlands in boreal continental Canada. *Canadian Journal of Botany* 71:10-22.

Lafleur PM, Roulet NT and Admiral SW. 2001. Annual cycle of CO_2 exchange in a bog peatland. *Journal of Geophysical Research* 106:3071-3081.

Latter PM, Howson G, Howard DM and Scott WA. 1998. Long-term study of litter decomposition on a Pennine peat bog: which regression? *Oecologia* 113:94-103.

Lavoie M and Richard PJH. 2000. The role of climate on the developmental history of Frontenac Peatland, southern Québec. *Canadian Journal of Botany* 78:668-684.

Magnusson T. 1993. Carbon dioxide and methane formation in forest mineral and peat

soils during aerobic and anaerobic incubations. *Soil Biology and Biochemistry* 25:877-883.

Miller PC, Mangan R and Kummerow J. 1982. Vertical distribution of organic matter in eight vegetation types near Eagle Summit, Alaska. *Holarctic Ecology* 5:117-124.

Moore TR. 1994. Trace gas emissions from Canadian peatlands and the effect of climatic change. *Wetlands* 14:223-228.

Moore TR, Roulet NT and Waddington JM. 1998. Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. *Climatic Change* 40:229-245.

Pakarinen P and Vitt DH. 1974 The major organic components and caloric contents of high arctic bryophytes. *Canadian Journal of Botany* 52: 1151-1161.

Pitkänen A, Turunen J and Tolonen K. 1999. The role of fire in the carbon dynamics of a mire, eastern Finland. *The Holocene* 9:453-462.

Robinson SD and Moore TR. 1999. Carbon and peat accumulation over the past 1200 years in a landscape with discontinuous permafrost, northwestern Canada. *Global Biogeochemical Cycles* 13:591-601.

Rochefort L, Vitt DH and Bayley SE. 1990. Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. *Ecology* 71:1986-2000.

Saarinen T. 1996. Biomass and production of two vascular plants in a boreal mesotrophic fen. *Canadian Journal of Botany* 74:934-938.

Scanlon D and Moore T. 2000. Carbon dioxide production from peatland soil profiles: The influence of temperature, oxic/anoxic conditions and substrate. *Soil Science* 165:153-160.

Scheffer RA and Aerts R. 2000. Root decomposition and soil nutrient and carbon cycling in two temperate fen ecosystems. *Oikos* 91:541-549.

Sjörs H. 1950. Regional studies in North Swedish mire vegetation. *Botaniska Notiser* 173-222.

Sjörs H. 1991. Phyto- and necromass above and below ground in a fen. *Holarctic Ecology* 14:208-218.

Szumigalski AR and Bayley S. 1996a. Net above-ground primary production along a bog-rich fen gradient in central Alberta, Canada. *Wetlands* 16:467-476.

Szumigalski AR and Bayley SE. 1996b. Decomposition along a bog to rich fen gradient in central Alberta, Canada. *Canadian Journal of Botany* 74:537-581.

Szumigalski AR and Bayley SE. 1997. Net aboveground primary production along a peatland gradient in central Alberta in relation to environmental factors. *Écoscience* 4:385-393.

Tallis JH. 1983. Changes in wetland communities. Pages 311-347 in: Gore AJP. (editor). *Mires: swamp, bog, fen and moor: General studies*. Ecosystems of the World 4A. Elsevier Scientific Publishing Company. Amsterdam.

Tansley AG. 1939. *The British Islands and their Vegetation*. The University Press. Cambridge.

Taylor BRPD and Parsons WFJ. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70:97-104.

Thormann MN and Bayley SE. 1997a. Aboveground net primary production along a bog-fen-marsh gradient in southern boreal Alberta, Canada. *Ecoscience* 4:374-384.

Thormann MN and Bayley SE. 1997b. Decomposition along a moderate-rich fen-marsh peatland gradient in boreal Alberta, Canada. *Wetlands* 17:123-137.

Thormann MN, Bayley SE and Currah RS. 2001. Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta, Canada *Canadian Journal of Botany* 79:9-22.

Thormann MN, Szumigalski AR and Bayley SE. 1999. Aboveground peat and carbon accumulation potentials along a bog-fen-marsh wetland gradient in southern boreal Alberta, Canada. *Wetlands* 19:305-317.

Tolonen K, Vasander H, Damman AWH and Clymo RS. 1992. Rate of apparent and true carbon accumulation in boreal peatlands. Pages319-333 in: *Proceedings of the 9th International Peat Congress. 22-26 June 1992, Uppsala, Sweden.*

Tolonen K. 1967. Über die Entwicklung der Moore im finnischen Nordkarelien. *Annales Botanici Fennici* 4:219-416 .

Tolonen K and Turunen J. 1996. Accumulation rates of carbon in mires in Finland and implications for climate change. *The Holocene* 6:171-178.

Turetsky MR. 2002. *Carbon storage and decay in peatlands under varying permafrost regimes*. Ph.D. Thesis, University of Alberta. *In preparation.*

Turetsky MR, Wieder RK, Williams CJ and Vitt DH. 2000. Organic matter accumulation, peat chemistry and permafrost melting in peatlands of boreal Alberta. *Ecoscience* 7:379-392.

Turunen J, Tomppo E, Tolonen K and Reinikainen A. 2002. Estimating carbon accumulation rates of undrained mires in Finland - application to boreal and subarctic regions. *The Holocene* 12:69-80.

Updegraff K, Pastor J, Bridgham SD and Johnston CA. 1995. Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. *Ecological Applications* 5:151-163.

van Diggelen R, Molenaar WJ and Kooijman AM. 1996. Vegetation succession in a

floating mire in relation to management and hydrology. *Journal of Vegetation Science* 7:809-820.

Verhoeven JTA, Maltby E and Schmitz MB. 1990. Nitrogen and phosphorus mineralization in fens and bogs. *Journal of Ecology* 78:713-726.

Verhoeven JTA and Toth E. 1995. Decomposition of *Carex* and *Sphagnum* litter in fens: effect of litter quality and inhibition by living tissue homogenates. *Soil Biology and Biochemistry* 27:271-275.

Waddington JM and Roulet NT. 1996. Atmosphere-wetland carbon exchanges: Scale dependency of CO_2 and CH_4 exchange on the developmental topography of a peatland *Global Biogeochemical Cycles* 10:233-245.

Waksman SA and Stevens KR. 1928a. Contribution to the chemical composition of peat: I. Chemical nature of organic complexes in peat and methods of analysis. *Soil Science* 26:113-137.

Waksman SA and Stevens KR. 1928b. Contribution to the chemical composition of peat: II. Chemical composition of various peat profiles. *Soil Science* 26:239-251.

Walker D. 1970. Direction and rate in some British post-glacial hydroseres. Pages 117-139 in: Walker D and West RG. (editors). *Studies in the Vegetational History of the British Isles*. Cambridge University Press. Cambridge, UK.

Wallén B. 1986. Above and below ground dry mass of the three main vascular plants on hummocks on a subarctic peat bog. *Oikos* 46:51-56.

Warner BG, Clymo RS and Tolonen K. 1993. Implications of peat accumulation at Point Escuminac, New Brunswick. *Quaternary Research* 39:245-248.

Weber CA. 1908. Aufbau und Vegetation der Moore Norddeutschlands. *Englers Botanische Jahrbücher Beiblatt* 90:19-34.

Williams CJ, Yavitt JB, Wieder RK and Cleavitt NL. 1998. Cupric oxide oxidation products of northern peat and peat-forming plants. *Canadian Journal of Botany* 76:51-62.

Winkler MG. 1988. Effect of climate on development of two *Sphagnum* bogs in south-central Wisconsin. *Ecology* 69:1032-1043.

Witte HJL and van Geel B. 1985. Vegetational and environmental succession and net organic production between 4500 and 800 B.P. reconstructed from a peat deposit in the western Dutch coastal area (Assendelver Polder). *Review of Palaeobotany and Palynology* 45:239-300.

Yu Z, Vitt DH, Campbell C and Campbell ID. 2000. Pattern and processes of peat accumulation in continental rich fens: hypothesis and preliminary results. Pages 208-215 in: Rochefort L and Daigle J-Y. *Sustaining Our Peatlands*. Canadian Society of Peat and Peatlands and the International Peat Society. Québec, Canada.

Zoltai SC, Morrissey LA, Livingston GP and de Groot WJ. 1998. Effects of fires on carbon cycling in North American boreal peatlands. *Environmental Reviews* 6:13-24.

Zoltai SC, Siltanen RM and Johnson RD. 2000. *A wetland database for the western boreal, subarctic, and arctic regions of Canada*. Information Report NOR-X-368, Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre. Edmonton, Alberta.

Table 4.1: Nitrogen content of different peat types assumed by the model. Values are based on data from five sites in continental western Canada: Athabasca AB, Rainbow Lake AB, Jan Lake SK, Flintstone Lake MB and North Knife Lake MB. The classification of peat types used is the same as in Chapter 2 (cf. Fig. 2.6), except for bryophyte peat, which had to contain more than 60 % non-*Sphagnum* moss remains.

	nitrogen content (% ashless dry weight)		
Peat type	mean	SD	n
Sphagnum peat	0.92	0.38	53
bryophyte peat	1.15	N/A	2
woody peat	2.09	0.35	12
herbaceous peat	2.86	0.82	38

Table 4.2: Parameters manipulated during sensitivity analysis. Individual parameter values were increased or decreased by 25% relative to a base-line scenario. Adjustments in each case were in the direction that was expected to increase organic matter accumulation. All simulations were run over 10,000 years.

SYM	VARIABLE	BASE VALUE	-25%	+25%
N/A	lignin content (proportion of original litter mass)	0.2	N/A	0.25
Q_c	asymptotic lignocellulose quotient	0.45	N/A	0.5625
	N-moderated turnover rate (yr^{-1})			
$\alpha_{Nc,SOL}$	soluble fraction	0.7	0.525	N/A
$\alpha_{Nc,HOL}$	holocellulose	0.45	0.3375	N/A
$\alpha_{Sf,LIG}$	surface lignin turnover rate (yr^{-1})	0.05	0.0375	N/A
NPP_{total}	total NPP ($g \cdot m^{-2} \cdot yr^{-1}$)	800	N/A	1000
ρ*	anoxic:oxic ratio	0.05	0.0375	N/A
ω	water table depth (cm)	20	15	N/A
π*	pH factor	0.8	0.6	N/A

* The pH factor (π) and anoxic:oxic ratio (ρ) are both part of the oxic:anoxic decay multiplier Zoa. ρ affects anaerobic decay rates only, whereas π affects both aerobic and anaerobic rates.

Table 4.3: Parameterization for different litter types, surface decay rates and external decay modifiers used in static simulations. The litter-dependent nitrogen multiplier is calculated by the model using N-content values from Table 4.1 and a Nitrogen factor (θ) of 2. NPP_{bg}:NPP_{total} is the proportion of total NPP that is attributable to belowground productivity

Litter-dependent parameters

	herbaceous	woody	bryophyte	*Sphagnum*
proportion SOL	0.3	0.3	0.21-0.29*	0.21-0.29*
proportion HOL	0.5	0.5	0.5	0.5
proportion LIG	0.2	0.2	0.21-0.29*	0.21-0.29*
Q_c	0.35	0.45	0.45	0.55
NPP_{bg} : NPP_{total}	0.4	0.75	N/A	N/A
N-multiplier	1.0	0.80	0.60	0.5

Surface turnover rates (yr^{-1})

	SOL	HOL	LIG
α_{Sf}	0.7	0.45	0.05

Parameters contributing to Zoa

	pH7	pH4
π	1.0	0.7
ρ	0.1	0.025

* LIG and SOL content of non-vascular litters depended on water table depth, with LIG = 0.21, SOL = 0.29 at ω = 5 cm; LIG = 0.25, SOL = 0.25 at ω = 25 cm; and LIG = 0.29, SOL = 0.21 at ω = 45 cm

Table 4.4: Ability of individual input parameters to increase peat accumulation over different timescales. Values represent percent increase in mass accumulation relative to the baseline scenario. For parameter values used, see Table 4.2.

		years since peat initiation									
SYM	VARIABLE	5	10	50	100	200	500	1000	2000	5000	10,000
N/A	original lignin content	14	20	32	36	46	62	61	59	55	51
Q_c	asymptotic lignocellulose quotient	7	15	33	40	53	71	71	69	65	61
α_{Nc}	N-moderated turnover rates (yr^{-1})	10	10	6	5	4	5	5	4	3	3
$\alpha_{Sf,LIG}$	surface lignin turnover rate (yr^{-1})	1	3	11	17	24	37	38	40	41	40
NPP_{total}	total NPP ($g \cdot m^{-2} \cdot yr^{-1}$)	28	30	33	36	45	59	57	55	51	47
ρ	anoxic:oxic ratio	0	0	0	0	0	1	4	6	10	14
ω	water table depth (cm)	1	2	4	9	20	36	36	33	28	23
π	pH factor	11	13	17	22	30	42	44	44	44	44

Table 4.5: Total NPP ($g \cdot m^{-2} \cdot yr^{-1}$), relative contribution of different vegetation types, and turnover rates (α; yr^{-1}) for static simulations. Turnover rates refer to the proportion of total mass lost from each litter type during the first year of the simulation, i.e., they represent surface 'litter bag' rates for fresh litter.

				Herbaceous		Woody		bryophytes		*Sphagnum*	
Peatland type	pH	ω	NPP_{total}	%NPP	α	%NPP	α	%NPP	α	%NPP	α
rich fens											
wet	6.5	5	983	79	0.32	11	0.26	9	0.17	2	0.15
medium	6.5	25	1012	60	0.43	22	0.35	7	0.20	11	0.16
dry	6.5	45	827	44	0.43	26	0.35	7	0.16	23	0.12
transitional fens											
wet	5.5	5	1076	79	0.28	10	0.23	9	0.15	2	0.13
medium	5.5	25	834	53	0.39	25	0.31	8	0.18	15	0.14
dry	5.5	45	917	48	0.38	29	0.31	7	0.15	17	0.15
bogs / poor fens											
wet	4.5	5	790	53	0.24	14	0.19	4	0.13	29	0.12
medium	4.5	25	621	35	0.34	28	0.28	4	0.16	33	0.13
dry	4.5	45	626	25	0.34	36	0.28	7	0.13	32	0.10

Table 4.6: Parameter estimates for fitted Clymo-type models in non-static simulations. Curves were fitted to 12 points at 500-year intervals from 'concave' profiles in Figure 4.11c, assuming the 'linear' decay rule of Clymo *et al.* (1998).

Final conditions		parameter estimates		Standard Errors		
pH	ω (cm)	p ($kg \cdot m^{-2} \cdot yr^{-1}$)	α (yr^{-1})	p	α	R^2
6.0	10	0.2390	0.001872	0.0011	0.000015	1.0000
4.5	10	0.3279	0.001728	0.0279	0.000258	0.9895
4.5	20	0.1577	0.000926	0.0071	0.000085	0.9966
4.5	30	0.0833	0.000498	0.0011	0.000016	0.9997

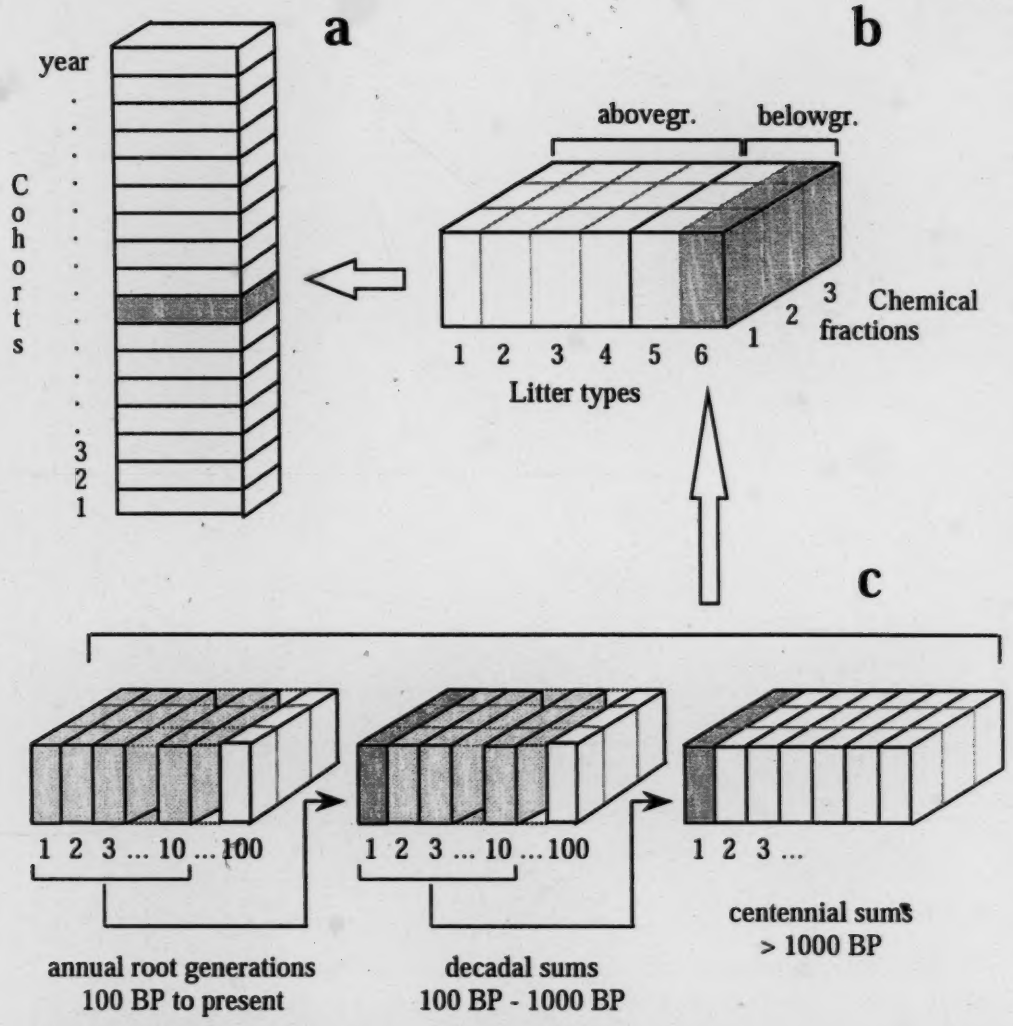


Figure 4.1: Partitioning of organic matter within the peat column. **(a)** The model follows the fate of a series of annual peat cohorts, with a new cohort *i* being initiated in each year of the simulation. **(b)** Each cohort contains six litter types, and mass for each litter type is subdivided into three chemical fractions. Litters 1 to 4 store herbaceous, woody, bryophyte and *Sphagnum* remains from aboveground NPP. These litters receive mass input only while the cohort is a the surface. Litters 5 and 6 store belowground remains of herbaceous and woody taxa and receive mass input as long as the cohort is within the rooting zone. **(c)** Within a cohort, mass for each of the belowground litters is subdivided depending on when it was added to the cohort. Annual generations of root input are tracked for 100 years. Mass that is older than 100 years is summarized into 10-year bins, and these are summarized again after 1000 years.

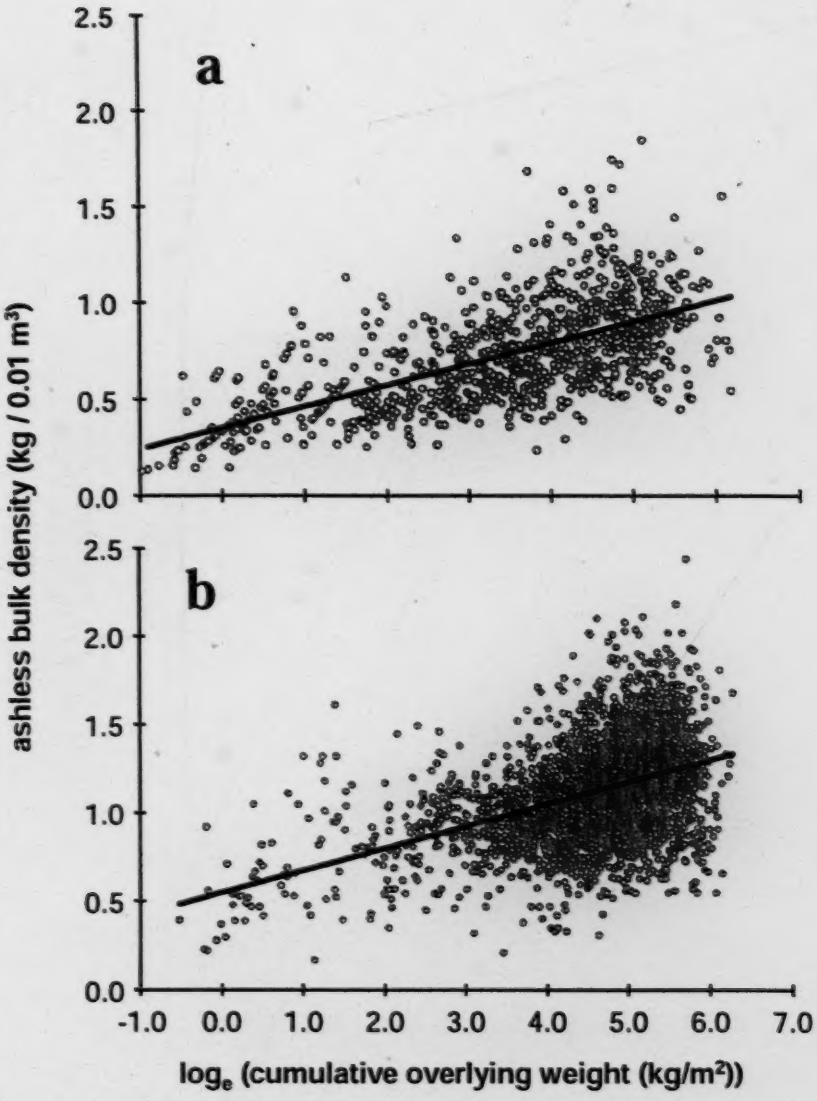


Figure 4.2: Relationship between weight of overlying material and the bulk density of different litter types (data from the ZPD; Zoltai *et al.* 2000). (a) bryophyte and *Sphagnum* peat. $R^2 = 0.40$, $p < 0.001$ (b) herbaceous and woody peat. $R^2 = 0.19$, $p < 0.001$. Only samples with < 20% ash content were included.

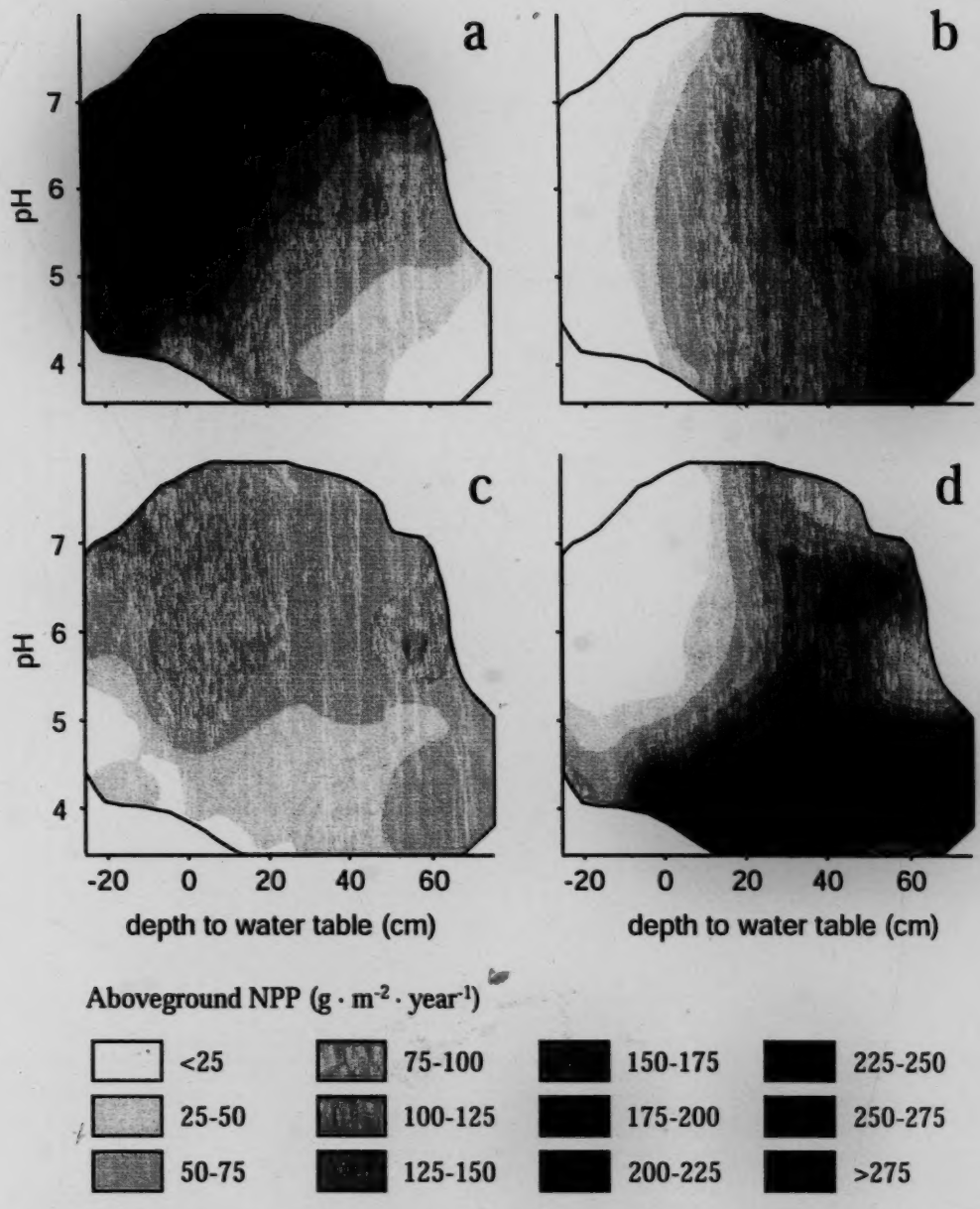


Figure 4.3: Aboveground NPP of different vegetation components as a function of surface water pH and water table depth. **(a)** herbaceous; **(b)** woody; **(c)** non-*Sphagnum* bryophytes; **(d)** *Sphagnum*. Cover abundance values are calculated by weighted averaging of surrounding data points from the ZPD (Zoltai *et* al. 2000) and converted to NPP using simple conversion factors (see text). Lattice points that have less than five data points within the search radius are left blank.

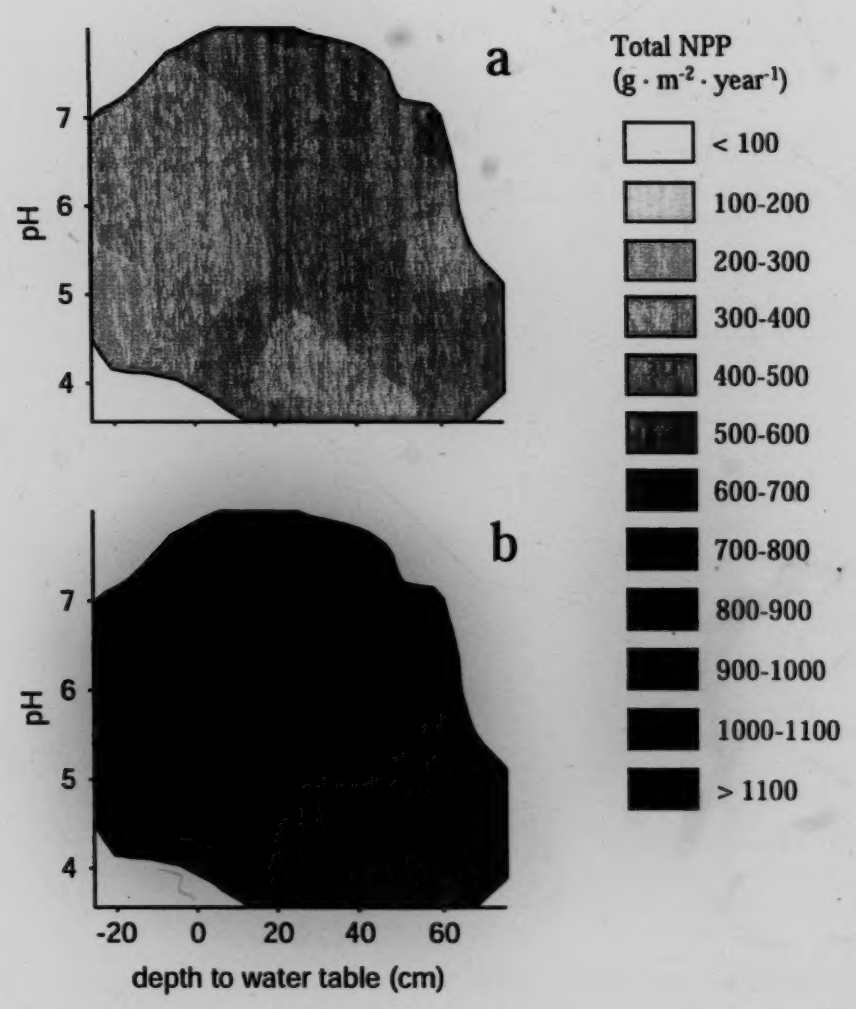


Figure 4.4: **(a) aboveground and (b) total NPP as a function of pH and water table depth. Aboveground NPP is calculated by summing the four vegetation components shown in Figure 4.3. Calculation of belowground NPP assumes fixed aboveground : belowground ratios for herbaceous and woody vegetation. Values shown in (b) assume that 40% and 75% of woody and herbaceous NPP (respectively) occur below ground.**

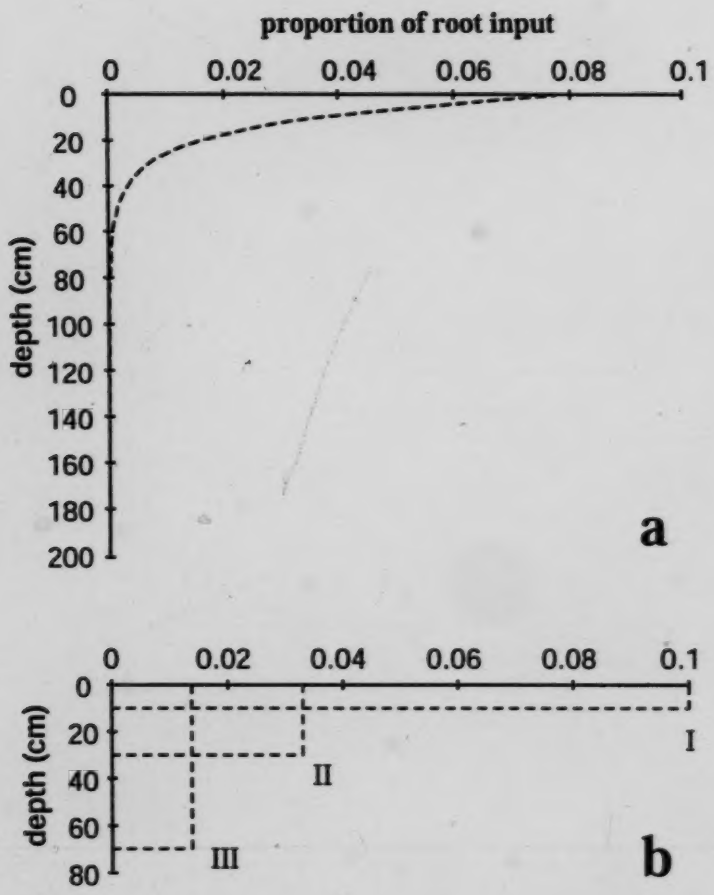


Figure 4.5: Vertical distribution of (a) herbaceous and (b) woody belowground NPP assumed by the model. Herbaceous root and rhizome mass decreases exponentially with depth, with 80% of annual inputs occurring within the upper 20 cm of peat. However, some herbaceous roots penetrate to depths of up to 200 cm. Woody roots and rhizomes are distributed evenly up to a maximum rooting depth that is determined annually based on water table position. If the water table is within 10 cm of the peat surface, woody rooting depth is 10 cm, otherwise it equals water table depth. Graphs shown in (b) correspond to rooting depths of 10 (I), 30 (II) and 70 (III) cm.

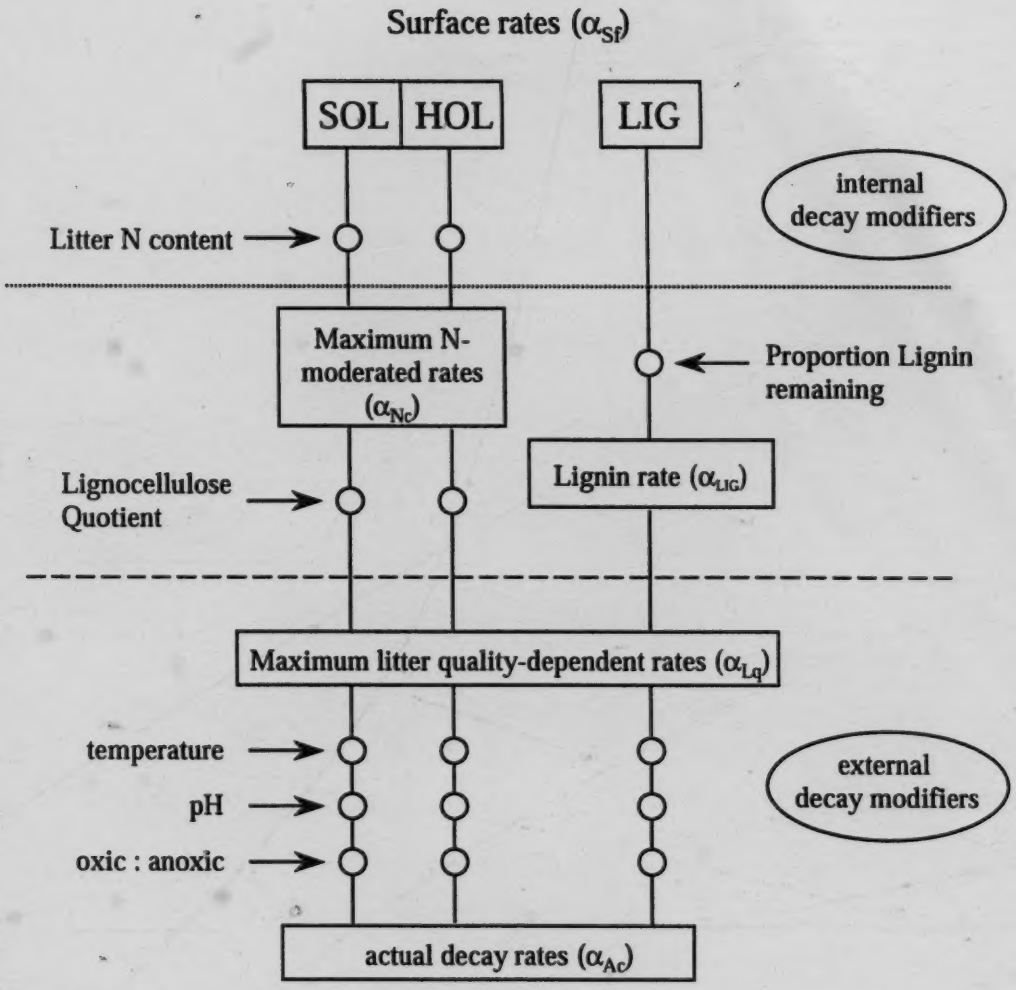


Figure 4.6: Overview over adjustments made to user-specified surface turnover rates for the three chemical fractions recognized by the model. Rates for soluble compounds and holocellulose are adjusted for litter N content at initialization. Subsequently, they are modified annually based on the lignocellulose quotient of the litter. Lignin turnover is not affected by nitrogen, but declines linearly as lignin mass decreases relative to its original value. All three chemical fractions are affected equally by external decay modifiers (temperature, pH and oxygen availability), which are calculated annually based on hydrological parameters and the stratigraphic position of each cohort.

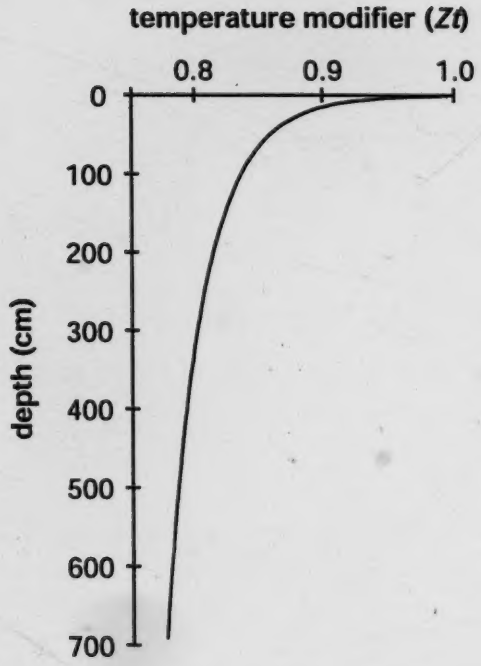


Figure 4.7: Changes in the temperature modifier (*Zt*) with depth

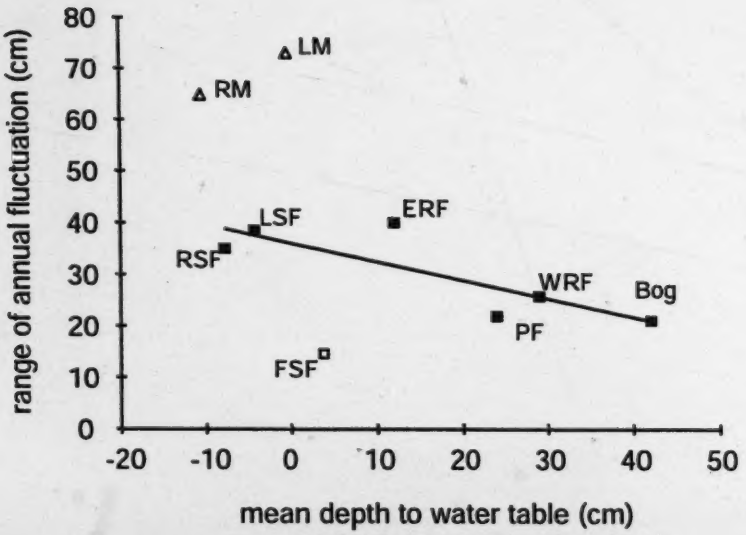
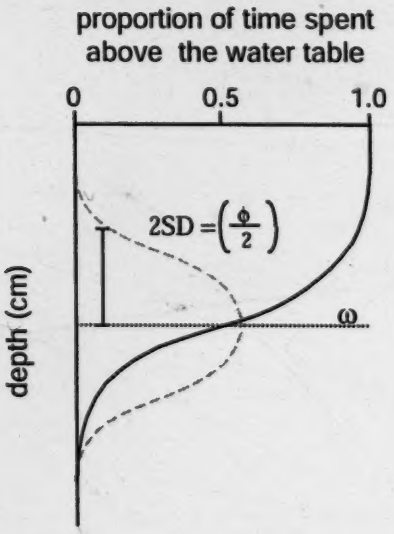


Figure 4.8: (a) Relationship between mean water table depth and range of (annual) fluctuations assumed by the model. The regression line shown ($R^2 = 0.68$, $p = 0.043$) was fitted to data points depicted as filled squares. (RSF: riverine sedge fen; LSF: lacustrine sedge fen; ERF: extreme rich fen; PF: poor fen; WRF: wooded rich fen). Floating peatlands (FSF: floating sedge fen) and marshes (RM: riverine marsh; LM: lacustrine marsh) cannot be simulated. All points represent two-year observation periods, except LSF and Bog, which are averages of two 2-year periods. Data from Szumigalski and Bayley (1997); Thormann and Bayley (1997); Thormann *et al.* (1999).



(b) Proportion of time a cohort spends above the water table. In a given year *i*, water table position is assumed to be normally distributed around the mean water table (ω), with the amplitude of annual fluctuations (ϕ) inversely related to water table depth (see (a)). The proportion of time a cohort spends above the water table is predicted from the cumulative distribution function (solid line) for a normal distribution with mean = ω and 2SD= $\phi/2$; (stippled line).

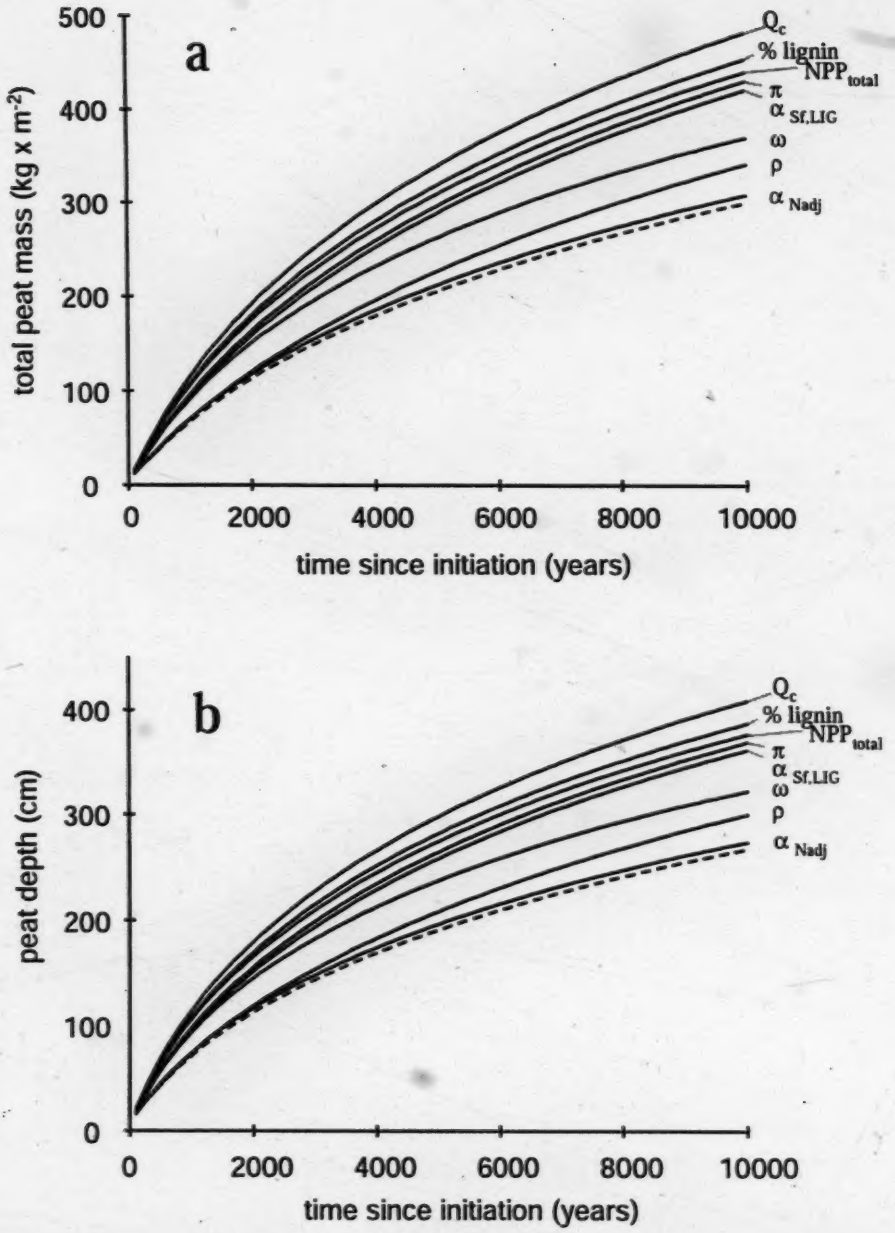


Figure 4.9: Peat accumulation by different scenarios tested during sensitivity analysis in terms of (a) mass, and (b) depth. The stippled line represents the base line case. Labels at the right refer to model parameters that were adjusted by 25% relative to base line values. For an explanation of symbols, refer to Table 4.2.

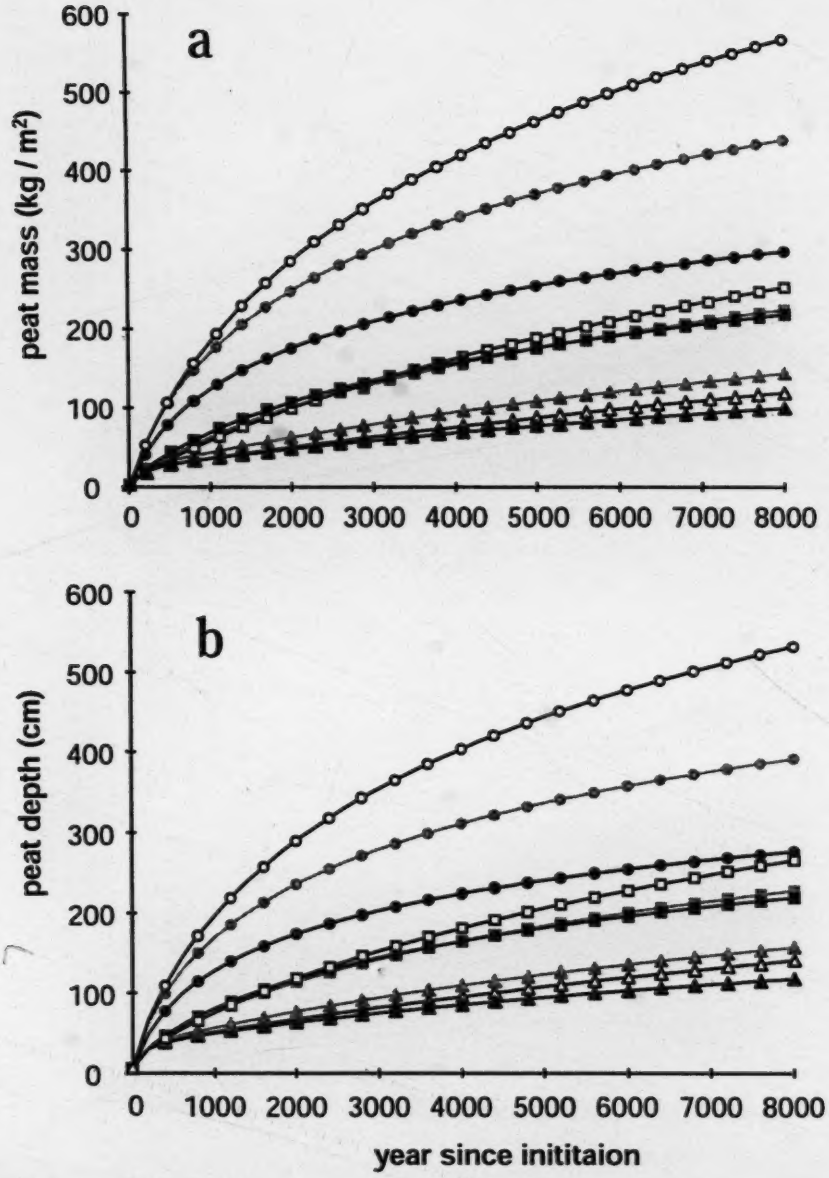


Figure 4.10: Changes in (a) peat mass and (b) depth over time in simulations with static water table and pH. ○ wet bog (ω = 5 cm, pH = 4.5); ● wet transitional fen (ω = 5 cm, pH = 5.5); ● wet rich fen (ω = 5 cm, pH = 6.5); □ medium bog (ω = 25 cm, pH = 4.5); ■ medium transitional fen (ω = 25 cm, pH = 5.5); ■ medium rich fen (ω = 25 cm, pH = 6.5); △ dry bog (ω = 45 cm; pH = 4.5); ▲ dry transitional fen (ω = 45 cm, pH = 5.5); ▲ dry rich fen (ω = 45 cm, pH = 6.5)

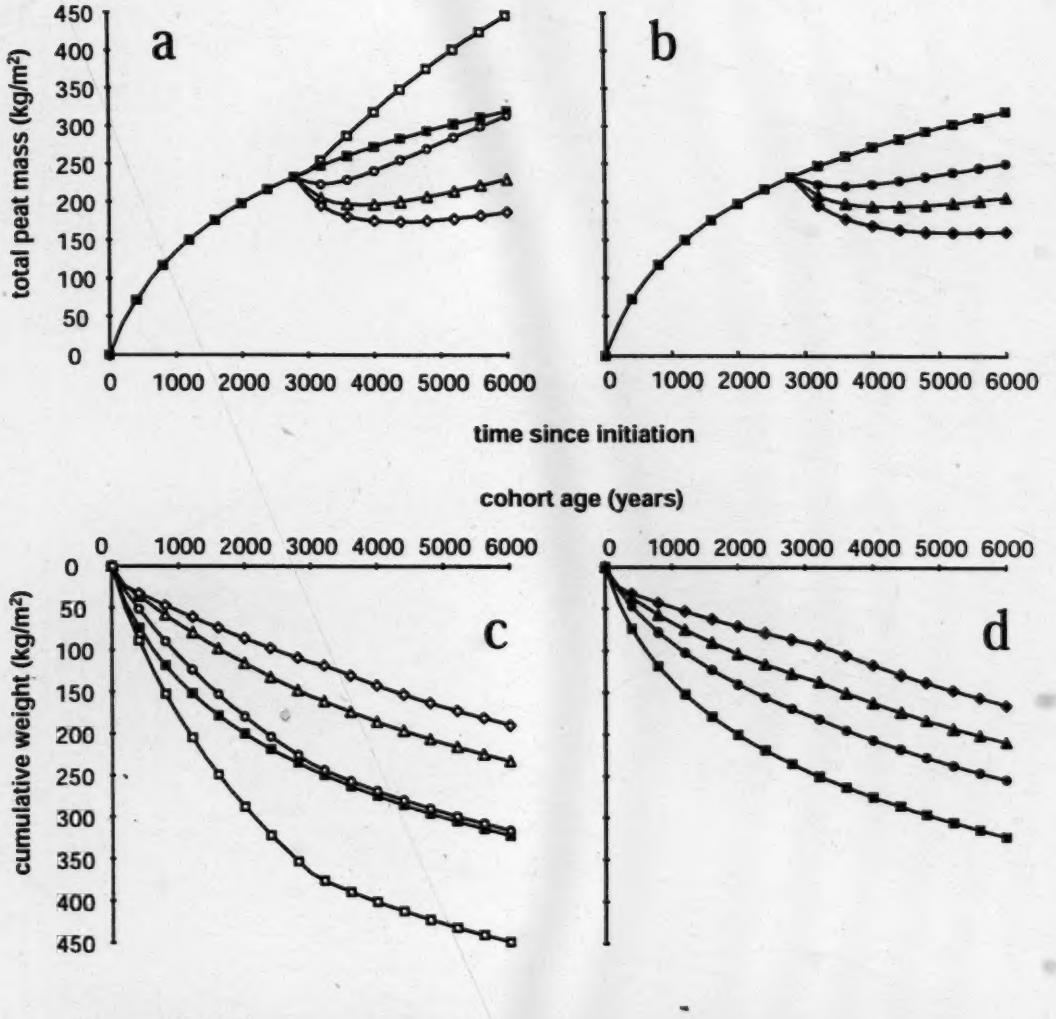


Figure 4.11: Effect of community transition on (a & b) mass accumulation over time, and (c & d) relationship between cohort age and cumulative overlying weight in final core profiles. All simulations were started as rich fens (pH = 6; ω = 10 cm). pH either remained constant throughout (filled symbols) or was decreased to a value of 4.5 between 2800 and 3000 years into the simulation (open symbols). At the same time, water table depth either remained constant (squares) or was dropped to 20 (circles), 30 (triangles), or 40 (diamonds) cm below the peat surface.

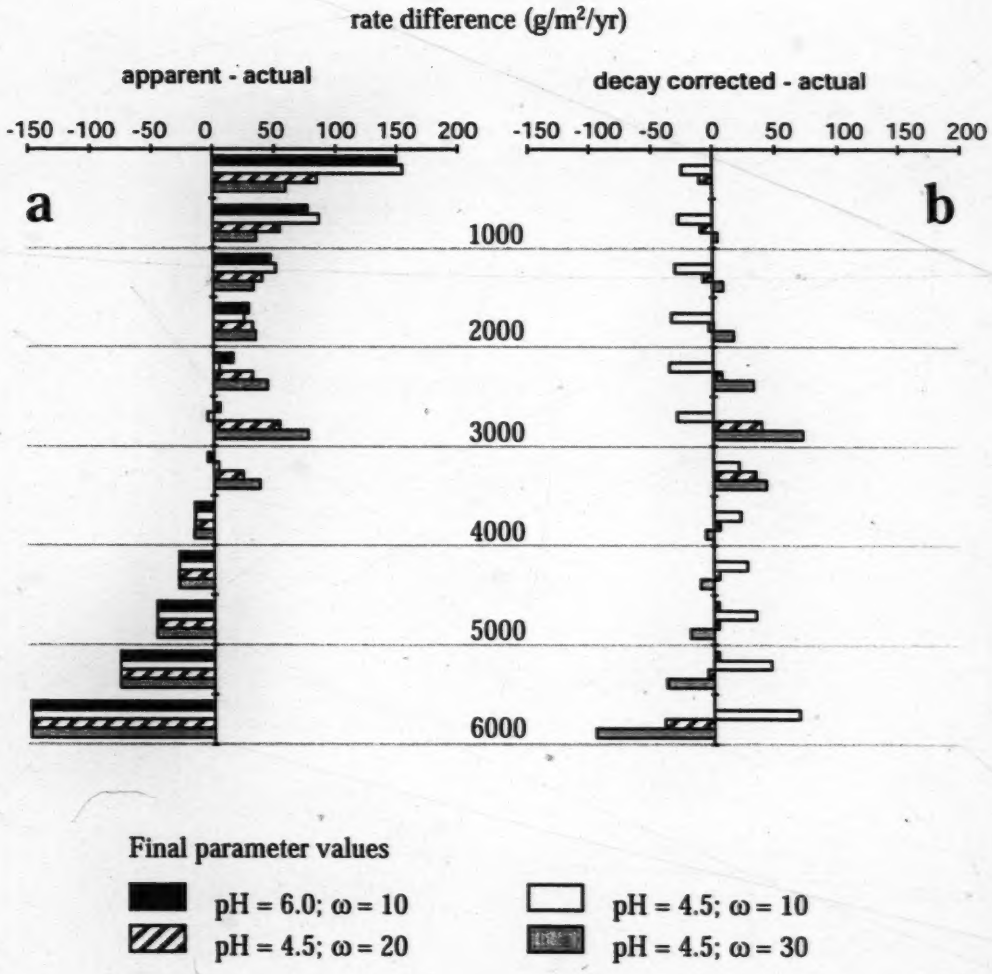


Figure 4.12: Difference between actual (net) rates of organic matter accumulation and rates inferred from core profiles. (a) apparent rates, (b) rates corrected for decay by fitting Clymo-type accumulation models (Table 4.6). The vertical axis represents time (years BP). All simulations were started with pH = 6 and ω= 10 cm. Between 3200 and 3000 years BP, parameters were adjusted to final values depicted in the legend.

CHAPTER 5

Overall Discussion and Conclusion

The results of this thesis depict peatland development as a highly dynamic process, with both vegetation development and organic matter accumulation controlled by complex interactions between internal and external forcing mechanisms. The autogenic model of vegetation succession (Weber 1908; Clements 1916) and the peat accumulation model proposed by Clymo (1984) are important conceptual tools that describe different aspects of peatland development within a set of idealized boundary conditions. In the case of Clymo model, these boundary conditions are well defined and include constant productivity, community composition and acrotelm depth (Clymo 1984). For autogenic succession, idealized boundary conditions would include availability of a suitable shallow lake basin, absence of external disturbance, and sufficient climatic moisture to permit ombrotrophication (cf. Chapter 1).

Simple conceptual models represent baseline scenarios against which observed patterns of peatland development should be evaluated. Departure from the predictions of these models can give us important clues about effects of altered boundary conditions, and can thus improve our functional understanding of peatland development. In the case of the autogenic model, this has been realized for some time. Kulczynski (1949), for example, remarked on the inability of Weber's (1908) autogenic model to explain patterns of peatland development in continental climates. He proposed a new conceptual framework that stressed the importance of landscape-scale patterns of water movement. Rigorous testing of conditions that may cause deviations from the concave cumulative mass / age profile predicted by the Clymo model (Clymo 1984) has only begun recently (Yu *et al.* 2000), and the consequences of violating model assumptions are generally not well understood.

Results of this thesis and the autogenic model

The results of this thesis clearly indicate that allogenic factors play a strong role in the development of continental peatlands. Topography, by controlling local patterns of water movement and availability, determines where peat initiates on a landscape. At both Athabasca and Rainbow Lake, initial peatland communities were

emergent marshes or fens that developed in physiographic positions where moisture was able to accumulate. At both sites, the onset of peat formation was probably triggered by climatic change, because it coincides with the end of early or mid-Holocene aridity (Vance 1986; Schweger and Hickman 1989). Most of the current peatland area was formed by paludification, and true limnic deposits composed of algal gyttya or remains of submerged aquatic macrophytes were not recovered, although they may exist in isolated localities. The low representation of basal limnic deposits is consistent with the results of other landscape-level studies from eastern North America (Heinselman 1970) and Fennoscandia (Aario 1932; Huikari 1956; Tolonen 1967).

In spite of their limited spatial extent, the initial foci of peat accumulation probably served as important catalysts for subsequent lateral expansion at both sites. The low hydraulic conductivity of peat affects local drainage patterns (Futyma and Miller 1986), and runoff from existing peatlands leads to flooding and expansion of peat onto surrounding mineral terrain (Aario 1932; Malmström 1932). At Rainbow Lake, the data available do not allow for reconstruction of directional patterns of expansion. In accordance with results of other studies (Korhola 1992; 1994; Almquist-Jacobson and Foster 1995), the speed and direction of early expansion at Athabasca were under strong local topographic control. In the southern fen basin, upslope expansion was a result of impeded drainage following peat accumulation farther downslope. This phenomenon has been observed previously (Korhola 1996; Charman 1994, Gauhl 1991, Foster and King 1984; Foster and Fritz 1987), and constitutes an example of autogenically driven paludification.

At Rainbow Lake, no lateral expansion is evident after 4000 BP, probably coinciding with regional establishment of permafrost. Many shallow peat deposits at Athabasca initiated within the past 3000 years. Whether this reflects hydrological change resulting from regional peatland expansion, impeded drainage following local soil development, or effects of climatic change is not clear. Most likely, a combination of several factors was involved. At both sites, basal peat deposits represent a variety of

different community types, with wet, monocot-dominated communities in the early Holocene. At Athabasca, there is a tend towards xeric, *Sphagnum* dominated basal deposits in later stages of lateral expansion. Similar patterns are evident from other studies that examined stratigraphies from both deep (central) and shallow (marginal) areas of the same site (Tolonen 1967; Futyma and Miller 1986; Korhola 1992; Klinger 1996). They suggest that hydrologic boundary conditions that trigger peat formation differ between developmental phases of the same peatland, and that autogenic effects increase in importance towards the later stages of paludification (Aario 1932; Klinger 1996).

Local patterns of community succession are variable at both sites. As predicted by the autogenic model, there is a trend towards *Sphagnum*-dominated communities in later stages of succession at Athabasca (Figure 2.9). However, individual cores differ in their basal community composition, and several display no or apparently reverse successional sequences. Most of these 'aberrant' patterns can be related to the physiographic position of individual core locations. Sites in the wet centre of the southern fen basin support moderate-rich fen communities that have changed little in the course of their development. At the margin of the fen basin, where water flow is less pronounced, *Sphagnum* is currently invading fen communities, whereas stagnant basins have been colonized by *Sphagnum* early in their development. At the northern margin of the fen basin, areas that originated by *Sphagnum* invasion into upland forest were subsequently flooded by geogenous water from the expanding fen, resulting in apparently reverse successional development.

Effects of topography are pronounced in the Athabasca site because it occupies several clearly defined basins that are situated on a gentle landscape gradient. The site is located in a region where atmospheric moisture may be limiting for peatland development (Gignac and Vitt 1994; Halsey *et al.* 1998) and ombrotrophication should occur less readily and only within favourable physiographic contexts. At Rainbow Lake, basin morphology is more complex, and its effects on community development are less apparent. Deep, isolated basins were occupied by monocot-dominated fens in

the early Holocene and subsequently invaded by *Sphagnum*. Periodic fires and permafrost dynamics have been the main determinants of community succession in recent times, and periods of autogenic vegetation development are punctuated by disturbance events.

Preferential establishment of permafrost in older, deeper peat has been observed previously (Kuhry 1998), but reasons for this phenomenon are not immediately apparent. As at Athabasca, lower current velocities in isolated basins may have allowed faster establishment of hummock Sphagna that are a prerequisite for tree establishment and permafrost development in the discontinuous zone (Zoltai 1993; Camill 1999; Robinson and Moore 2000). Greater water movement in surrounding fens would have prevented establishment of these key species, and fens consequently remained permafrost free. Furthermore, permafrost establishment in parts of the site may have altered drainage patterns and prevented subsequent community succession in non-permafrost areas. Neither of these hypotheses are testable using the data available, and landscape-level controls over peatland dynamics in regions of discontinuous permafrost need further investigation.

Patterns of organic matter accumulation and the Clymo model

Long-term apparent rates of peat (height) accumulation are highly variable in both sites examined. The low number of ^{14}C dates precludes rigorous analysis, but lower rates of organic matter accumulation in younger cores at Rainbow Lake most likely reflect the increasing influence of permafrost. Similar patterns have been observed at other sites (Vardy *et al.* 2000). In Athabasca, there is no relationship between core age and apparent accumulation rates. Rather, community composition seems to have played an important role in determining rates of organic matter accumulation, with fast rates in wet, moderate-rich fen communities, and slower accumulation in *Sphagnum*-dominated regions. Neither of these trends follows the pattern of bias inherent in the use of apparent rates, which predicts faster apparent accumulation rates in younger cores (Clymo *et al.* 1998; Chapter 4).

The applicability of the Clymo model to permafrost peatlands is questionable. Decomposition is likely to cease in permanently frozen peat, and traditional distinctions between acrotelm and catotelm (Ingram 1978) are unlikely to describe organic matter dynamics in permafrost sites where a water table may not be present above the permafrost (Vardy *et al.* 2000). The comparatively high frequency of peat fires in boreal and subarctic permafrost areas (Zoltai *et al.* 1998) and periodic cycles of permafrost collapse and re-aggradation Zoltai 1993, Chapter 3) further violate basic assumptions of the Clymo model. Even if multiple dates are available for individual core profiles, interpretation of changes in organic matter accumulation is complicated by the fact that peatland initiation often occurred in the absence of permafrost (Zoltai and Tarnocai 1975; Zoltai 1993), and it may not be possible to determine the exact timing of permafrost initiation from marcofossil data alone (Oksanen *et al.* 2001; Chapter 3).

Observed (Chapter 2) and modelled (Chapter 4) differences in peat accumulation potential between community types indicate that the assumptions of constant organic matter input and decay inherent in the Clymo (1984) model may be seriously violated in peatlands that undergo community transition. Since succession is the rule rather than exception in peatland development (Weber 1908; Clements 1916; Walker 1970; Tallis 1983), this has serious implications for the interpretation of cumulative mass / age profiles preserved in peat deposits. Simulation results (Chapter 4) demonstrate that 'concave' profiles like those predicted by the Clymo model may result even in sites that have experienced extended periods of net organic matter loss. This implies that fitting of 'Clymo-type' curves in order to infer past organic matter dynamics can produce misleading results, even if these models show a good fit to the data.

Yu *et al.* (2000) demonstrate that the 'convex' profiles documented for several peatland sites in continental western Canada most likely reflect decreasing organic matter input into the catotelm over time. Simulation results obtained here suggest that sudden changes in organic matter input can result in a variety of cumulative mass / age

profiles, and that 'flat' profiles, such as observed by e.g. Charman *et al.* (1994) and Belyea and Warner (1996) may reflect temporal changes in mass input that cannot be detected by fitting a Clymo-type model. Overall, the ubiquity of 'flat' and 'convex' profiles in continental peat deposits suggests that decreases in net organic matter accumulation at many sites have been greater than predicted by the Clymo model. This conclusion is supported, albeit less rigorously, by the lack of a relationship between core age and apparent rates of height accumulation at the Athabasca site.

Peatland response to future climate change

In order to predict future effects of climatic change on the carbon dynamics of peatlands, we need a more dynamic approach to the interpretation of core records that incorporates the effect of vegetation change on organic matter accumulation. This will require a combination of modelling and paleoecological analysis, as well as improved understanding of the relative importance of plant-mediated and environmental parameters in controlling decomposition in peatlands. Patterns of community development and associated differences in peat accumulation rates at the Athabasca site suggest that effects of climatic warming will be greatest in areas of shallow peat close to current peatland margins. In many such areas peat initiated comparatively recently, and present hydrological boundary conditions appear marginal for peat accumulation. In the discontinuous permafrost zone, effects of climate change on peatland carbon dynamics will be strongly linked to the fate of permafrost, and hydrological consequences of permafrost degradation will be of critical importance in determining future patterns of organic matter accumulation at both local and regional scales..

Conclusion

The results of this thesis indicate that autogenic succession plays an important role in the development of continental peatlands. Allogenic factors impart strong constraints during site initiation and play a large role in determining subsequent patterns of spatial expansion. They further affect both the speed and direction of local

successional pathways. Peat core data and modelling results both indicate that vegetation-dependent and environmental differences between peatland communities have strong implications for organic matter accumulation, and that few natural peatlands are likely to fit the stringent assumptions inherent in the Clymo model.

Overall, the results of the work described here provide several insights that should be considered in future studies of continental peatlands:

1) Fens do not have inherently low peat accumulation potential. Results from the Athabasca site demonstrate that fens can accumulate peat extremely rapidly, at least in physiographic contexts that allow for local water tables to 'track' peat accumulation. Although it is unclear how representative the site is of the region as a whole, fens in continental western Canada currently store twice as much carbon as bogs (Vitt *et al.* 2000). Factors that control peat accumulation in fens need to be considered in more detail.

2) Given the dominance of fens in continental regions, studies of peatland distribution and development have to explicitly consider landscape hydrology. In order to understand and predict the distribution of different community types, we not only need to understand their relationships to local water tables and surface water chemistry, but also what controls the distribution of such 'boundary conditions' within a landscape.

3) The fitting of simple mathematical models such as the Clymo model to core profiles is not recommended in sites that have undergone community change. At best, such models provide a bad fit to observed cumulative mass / age profiles. However, good fits may be obtained even if basic model assumptions have been violated, leading to incorrect conclusions about past carbon dynamics. Lack of sensitivity to violation of their basic assumptions means that such models cannot be reliably tested against field data.

LITERATURE CITED

Aario L. 1932. Pflanzentopographische und paläogeographische Mooruntersuchungen in N-Satakunta. *Fennia* 55:1-179.

Almquist-Jacobson H and Foster DR. 1995. Toward an integrated model for raised-bog development: Theory and field evidence. *Ecology* 76:2503-2516.

Belyea LR and Warner BG. 1996. Temporal scale and the accumulation of peat in a *Sphagnum* bog. *Canadian Journal of Botany* 74:366-377.

Camill P. 1999. Peat accumulation and succession following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Écoscience* 6:592-602.

Charman DJ. 1994. Patterned fen development in northern Scotland: developing a hypothesis from palaeoecological data. *Journal of Quaternary Science* 9:285-297.

Charman DJ, Aravena R and Warner BG. 1994. Carbon dynamics in a forested peatland in north-eastern Ontario, Canada. *Journal of Ecology* 82:55-62.

Clements FE. 1916. *Plant Succession: An analysis of the development of vegetation.* The Carnegie Institution of Washington. Washington.

Clymo RS. 1984. The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London* B 303:605-654.

Clymo RS, Turunen J and Tolonen K. 1998. Carbon accumulation in peatland. *Oikos* 81:368-388.

Foster DR and Fritz SC. 1987. Mire development, pool formation and landscape processes on patterned fens in Dalarna, Central Sweden. *Journal of Ecology* 75:409-437.

Foster DR and King GA. 1984. Landscape features, vegetation and developmental

history of a patterned fen in south-eastern Labrador, Canada. *Journal of Ecology* 72:115-143.

Futyma RP and Miller NG. 1986. Stratigraphy and genesis of the Lake Sixteen peatland, northern Michigan. *Canadian Journal of Botany* 64:3008-3019.

Gauhl F. 1991. Untersuchungen zur Entwicklung des Schwarzen Moores in der Rhön: Verlauf und Ursachen der Vermoorung. *Flora* 185:1-16.

Gignac LD and Vitt DH. 1994. Responses of northern peatlands to climate change: Effects on bryophytes. *Journal of the Hattori Botanical Laboratory* 75:119-132.

Halsey LA, Vitt DH and Bauer IE. 1998. Peatland initiation during the Holocene in Continental Western Canada. *Climatic Change* 40:315-342.

Heinselman ML. 1970. Landscape evolution, peatland types and the environment in the Lake Agassiz Peatlands Natural Area, Minnesota. *Ecological Monographs* 40:235-261.

Huikari O. 1956. Primmäärisen soistumisen osuudesta Suomen soiden synnyssä (Untersuchungen über den Anteil der primären Versumpfung an der Entstehung der Finnischen Moore). *Communicationes Instituti Forestalis Fenniae* 46:1-79.

Ingram HAP. 1978. Soil layers in mires: function and terminology. *Journal of Soil Science* 29:224-227.

Klinger LF. 1996. The myth of the classic hydrosere model of bog succession. *Arctic and Alpine Research* 28:1-9.

Korhola A. 1992. Mire induction, ecosystem dynamics and lateral extension on raised bogs in the southern coastal area of Finland. *Fennia* 170:25-94.

Korhola A. 1996. Initiation of a sloping mire complex in southwestern Finland: autogenic versus allogenic controls. *Écoscience* 3:216-222.

Korhola AA. 1994. Radiocarbon evidence for rates of lateral expansion in raised mires in southern Finland. *Quaternary Research* 42:299-307.

Kuhry P. 1998. Late Holocene permafrost dynamics in two subarctic peatlands of the Hudson Bay Lowlands (Manitoba, Canada). *Eurasian Soil Science* 31:529-534.

Kulczynski MSt. 1949. Torfowiska Polesia: Peat bogs of Polesie. *Mémoires de l'Académie Polonaise des Sciences et des Lettres. Classe des Sciences Mathématiques et Naturelles Serie B: Sciences Naturelles* 15:1-356.

Malmström C. 1932. Om faran för skogsmarkens försumpning i Norrland (Über die Gefahr der Versumpfung des Waldbodens in Norrland (Nordschweden)). *Meddelanden från Statens Skogsförsöksanstalt* 26:1-162.

Oksanen PO, Kuhry P and Alekseeva RN. 2001. Holocene development of the Rogavaya River peat plateau, European Russian Arctic. *The Holocene* 11:25-40.

Robinson SD and Moore TR. 2000. The influence of permafrost and fire upon carbon accumulation in High Boreal peatlands, Northwest Territories, Canada. *Arctic, Antarctic and Alpine Research* 32:155-166.

Schweger CE and Hickman M. 1989. Holocene paleohydrology of central Alberta: testing the general-circulation-model climate simulations. *Canadian Journal of Earth Sciences* 26:1826-1833.

Tallis JH. 1983. Changes in wetland communities. Pages 311-347 in: Gore AJP. editor. *Mires: swamp, bog, fen and moor: General studies*. Ecosystems of the World Volume 4A. Elsevier Scientific Publishing Company. Amsterdam.

Tolonen K. 1967. Über die Entwicklung der Moore im finnischen Nordkarelien. *Annales Botanici Fennici* 4:219-416 .

Vance RE. 1986. Pollen stratigraphy of Eaglenest Lake, northeastern Alberta. *Canadian Journal of Earth Sciences* 23:11-20.

Vardy SR, Warner BG, Turunen J and Aravena R. 2000. Carbon accumulation in permafrost peatlands in the Northwest Territories and Nunavut, Canada. *The Holocene* 10:273-280.

Vitt DH, Halsey LA, Bauer IE and Campbell C. 2000. Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. *Canadian Journal of Earth Sciences* 37:683-693.

Walker D. 1970. Direction and rate in some British post-glacial hydroseres. Pages 117-139 in: Walker D and West RG. (editors). *Studies in the Vegetational History of the British Isles.* Cambridge University Press. Cambridge, UK.

Weber CA. 1908. Aufbau und Vegetation der Moore Norddeutschlands. *Englers Botanische Jahrbücher* Beiblatt 90:19-34.

Yu Z, Vitt DH, Campbell C and Campbell ID. 2000. Pattern and processes of peat accumulation in continental rich fens: hypothesis and preliminary results. Pages 208-215 in: Rochefort L and Daigle J-Y. *Sustaining Our Peatlands*. Canadian Society of Peat and Peatlands and the International Peat Society. Québec, Canada.

Zoltai SC. 1993. Cyclic development of permafrost in the peatlands of Northwestern Alberta, Canada. *Arctic and Alpine Research* 25:240-246.

Zoltai SC, Morrissey LA, Livingston GP and de Groot WJ. 1998. Effects of fires on carbon cycling in North American boreal peatlands. *Environmental Reviews* 6:13-24.

Zoltai SC and Tarnocai C. 1975. Perennially frozen peatlands in the western Arctic and Subarctic of Canada. *Canadian Journal of Earth Sciences* 12:28-43.

APPENDIX 1

Relationship between landforms shown in Figures 2.2 and 3.3 and wetland types recognized by the Alberta Wetland Inventory Classification Standards

Landforms shown in Figures 2.2 and 3.3 are based on wetland types recognized by the Alberta Wetland Inventory Classification Standards (Halsey and Vitt 1997). The tables presented in this Appendix list the wetland types that comprise the different landforms shown at each site. For detailed descriptions of the wetland types, as well as guidelines regarding their identification from aerial photographs, see Vitt *et al.* (1996); Halsey and Vitt (1997).

Halsey LA and Vitt DH. 1997. Alberta Wetland Inventory Standards. In: *Alberta Vegetation Inventory Standards Version 2.0.* Resource Data Division, Alberta Environmental Protection.

Vitt DH, Halsey LA, Thormann MN and Martin T. 1996. *Peatland Inventory of Alberta.* Alberta Peat Task Force, Network of Centres of Excellence in Sustainable Forest Management Grant, University of Alberta, Edmonton, Alberta

Table A1.1: Mapped wetland types and corresponding landform designations used in Figure 2.2 (Athabasca).

Landform designation in Figure 2.2	Wetland type (AVI)	Description
bog	BTNN	Wooded bogs without internal lawns
open fen	FONS	Nonpatterned, open, shrub-dominated fens
swamp	STNN	coniferous swamps
treed fen	FTNN	nonpatterned, wooded fens with no internal lawns

Table A1.2: Mapped wetland types and corresponding landform designations used in Figure 3.3 (Rainbow Lake).

Landform designation in Figure 3.3	Wetland type (AVI)	Description
bog	BTXC	wooded permafrost bogs with collapse scars
	BTXN	wooded permafrost bogs without collapse scars
shrubby fen	FONS*	nonpatterned, open, shrub-dominated fens
swamp	STNN	coniferous swamps
	SONS*	deciduous swamps
treed fen	FTNN	nonpatterned, wooded fens with no internal lawns

* FONS and SONS are both characterized by >25% shrub cover. These wetland types generally occupy different landscape positions, but shrub height is one of the features used to distinguish them on aerial photographs (with *Salix* spp. generally above shoulder height in deciduous swamps). Since photographs used for mapping at this site were taken eight years after a fire, there may be some inaccuracies in the delineation of these landform types.

APPENDIX 2

Reference material used in macrofossil determination and concepts used for identification of important macrofossil taxa

REFERENCE MATERIAL USED

(a) Bryophytes

The general keys provided in many of these sources are not suitable for the identification of macrofossil remains because key features (such as stem leaves of *Sphagnum* spp.) are generally not preserved. However, descriptions and diagrams contained in these sources are invaluable for comparison among a limited number of candidate taxa, and some of the taxonomically more restricted keys (especially keys to the Amblystegiaceae in Crum and Anderson (1981) and keys to genera such as *Drepanocladus* and *Calliergon* in Crum and Anderson (1981) and Lawton (1971)) can be useful for the identification of bryophyte macrofossils from peatlands.

Crum HA and Anderson LE. 1981. *Mosses of Eastern North America.* 2 Volumes. Columbia University Press, New York.

Crum HA. 1984. Sphagnopsida, Sphagnaceae. *North American Flora*, Series II Part 11. New York Botanical Garden, Bronx, New York.

Janssens JA. 1983. Past and extant distribution of *Drepanocladus* in North America, with notes on the differentiation of fossil fragments. *Journal of the Hattori Botanical Laboratory* 54:251-298.

Lawton E. 1971. *Moss Flora of the Pacific Northwest.* The Hattori Botanical Laboratory, Nichinan, Miyazaki, Japan.

Natural Environment Research Council, Institute of Terrestrial Ecology. 1990. *Handbook of European Sphagna.* HMSO, London.

Smith AJE. 1978. *The Moss Flora of Britain & Ireland.* Cambridge University Press, Cambridge.

Smith AJE. 1990. *The Liverworts of Britain & Ireland.* Cambridge University Press, Cambridge.

Vitt DH and Andrus RE. 1977. The genus *Sphagnum* in Alberta. *Canadian Journal of Botany* 55:331-357.

(b) Other remains

These sources generally provide more detail than was used in the present study. Pictures, descriptions and diagrams were used mainly to help in the interpretation of vascular plant remains and for identification of distinct macrofossil types that are not necessarily mentioned in the text.

Core HA, Côte WA and Day AC. 1979. *Wood Structure and Identification.* 2nd edition. Syracuse University Press, Syracuse, New York.

Grosse-Brauckmann G. 1972. Über pflanzliche Makrofossilien mitteleuropäischer Torfe I. Gewebereste krautiger Pflanzen und ihre Merkmale. *Telma* 2:19-55.

Grosse-Brauckmann G. 1974. Über pflanzliche Makrofossilien mitteleuropäischer Torfe II. Weitere Reste (Früchte und Samen, Moose u.a.) und ihre Bestimmungsmöglichkeiten. *Telma* 4:51-117.

Lévesque PEM, Dinel H, and Larouche A. 1988. *Guide to the identification of plant macrofossils in Canadian peatlands.* Research Branch, Agriculture Canada Publication No. 1817.

van Geel B, Bohncke SJP and Dee H. 1981. A palaeoecological study of an upper Late Glacial and Holocene sequence from de Borchert, The Netherlands. *Review of Palaeobotany and Palynology* 31:367-448.

van Geel B, Hallewas DP and Pals JP. 1983. A late Pleistocene deposit under the Westfriese Zeedijk near Enkhuizen, province of Noord-Holland, The Netherlands. Palaeoecological and archaeological aspects. *Review of Palaeobotany and Palynology* 38:269-336.

CONCEPTS USED FOR IDENTIFICATION OF MAJOR MACROFOSSIL TAXA

(a) *Sphagnum*

Sphagnum angustifolium (Section *Cuspidata*)

Stems yellowish or white, without enlarged cortical cells. Stem leaves, if present, small and triangular. Branch leaves small (≤ 1.5 mm long), narrowly lanceolate, with hyaline cells extending into the tip of the leaf. Green cells of branch leaves ovate-triangular, broadly exposed on abaxial surface of leaf. Hyaline cells of spreading branch leaves long and narrow, abaxial surface usually with a single ±circular pore in the apical angle. In several specimens (from Rainbow Lake), some (1-3) small pores or pseudopores in lateral cell angles on the abaxial leaf surface.

Sphagnum fuscum / S. capillifolium (Section *Acutifolia*)

Stems usually dark (brown in *S. fuscum*), with well-developed cortex consisting of enlarged hyaline cells. No pores in outer layer of stem cortex (if preserved). Stem leaves, if present, lingulate, sometimes narrowing towards the base. Green cells of branch leaves ± triangular, broadly exposed on adaxial surface of the leaf and narrowly exposed on the abaxial side. Hyaline cells on abaxial surface of branch leaves with large pores in lateral cell angles that appear oval in surface view due to cell convexity. Towards the apex of branch leaves, pores become smaller and more rounded, but they remain larger than those of *S. warnstorfii* and lack the thick rings characteristic of that species. If only branch leaves are present or preservation is poor (which is often the case in basal samples from marginal sites), some other members of section *Acutifolia* (e.g. *S. russowii*) may be erroneously included in this group.

Sphagnum magellanicum (Section *Sphagnum*)

Stems, if present, with a well-developed (several cell layers thick) hyaline cortex; cortical cells with fibrils and circular pore(s) in the outer layer. Branch leaves large (usually > 1.5 mm long), broadly ovate, with a hooded (cucullate) tip. Green

cells of branch leaves small, oval in cross-section, and completely enclosed by adjacent hyaline cells.

Sphagnum riparium (Section *Cuspidata*)

Stems yellowish or white, without enlarged cortical cells. Stem leaves, if present, large, ovate-lingulate, with a pronounced split at the apex due to cell resorption. Branch leaves large (usually >2 mm long), lanceolate; hyaline cells not extending into the tip of the leaf, which is made up of simple, undifferentiated cells. Hyaline cells of spreading branch leaves with a large resorption gap in the apical cell angle, with abaxial surface lacking other pores.

Sphagnum warnstorfii (Section *Acutifolia*)

Stems variable in colour, with a well-developed cortex consisting of enlarged hyaline cells. No pores in outer layer of stem cortex (if preserved). Stem leaves, if present, lingulate. Green cells of branch leaves ± triangular, broadly exposed on the adaxial surface of the leaf and narrowly exposed on the abaxial side. Hyaline cells on the abaxial surface of branch leaves with small, round, strongly ringed pores, especially towards the leaf apex. Cells with ringed pores extend further towards the base in the leaf centre than at the margins. In lower parts of the leaf, especially towards the leaf margin, pores are large, and their patterning resembles that of *S. fuscum / S. capillifolium*. While typical leaves of this species are easily recognized, older or poorly preserved specimens can be hard to distinguish from *S. fuscum / capillifolium*. Borderline cases were generally assigned to *S. fuscum / S. capillifolium*.

(b) Other mosses

This list is restricted to common taxa. Species that occurred in only one or a few samples were identified with the help of resident experts and reference material (both herbarium specimens and prepared slides) from the Cryptogamic Herbarium at the University of Alberta (ALTA).

Aulacomnium palustre

Leaves lanceolate to lingulate, usually retaining a yellowish-green color even in deep peat samples. Leaf margins entire except towards the apex. Costa ends slightly below the leaf apex. Leaf cells ± isodiametric, thick-walled, with one large papilla on each leaf surface. Stems, if present, with brown tomentum.

Bryum pseudotriquetrum

Leaves variable in size, oblong-lanceolate to ovate-lanceolate, usually decurrent at the base. Costa strong, extending to or beyond the leaf apex. Cells rectangular at leaf base, ± rhomboid towards the apex. Leaf margins recurved and entire at base, often serrulate towards apex. Leaves may be bordered by several rows of linear, thick-walled cells. Stems, if present, bright red, often with brown tomentum.

Calliergon giganteum

Stem leaves broad (cordate-ovate) and hooded at the apex, the costa extending almost to the apex of the leaf. Branch leaves (which are more abundant in peat samples) are narrower (oval), with a shorter costa and inrolled margins towards the apex. Cells linear throughout most of the leaf; shorter and broader close to the apex, often with several clear cells that used to bear rhizoids. Alar cells abruptly inflated to form large, decurrent auricles.

Hamatocaulis vernicosus

Leaves falcate-secund, lanceolate to ovate-lanceolate, acuminate. Margins entire. The costa extends beyond the middle of the leaf. Cells linear except at leaf base; alar cells undifferentiated. Stems with an outer layer of small cells; central strand absent.

Meesia triquetra

Leaves ovate-lanceolate, spreading to almost squarrose, keeled, gradually tapering towards the acumen. Costa strong, ending just below the apex. Cells ±

rectangular, longer at the leaf base that at the apex. Margins distinctly serrulate, often from close to the leaf base. Stems, if present, often with tomentum.

Pohlia nutans / sphagnicola

Leaves oval-lanceolate, acute, not or only slightly decurrent. Costa strong, extending almost to the apex. Leaf margins entire, denticulate towards apex. Leaves not bordered. Cells rectangular to linear-rhomboidal. Specimens from the Rainbow Lake site have relatively small, ovate leaves with comparatively short cells and faintly denticulate margins.

Polytrichum strictum

Leaves with a sheathing base that abruptly narrows to a narrowly lanceolate, acuminate blade. Midrib broad, covered by lamellae that are 5-7 cells high. Lamina narrow and folded over midrib; margins entire. Costa excurrent, with teeth on abaxial side. Lower regions of stem covered by dense white tomentum. Stems are distinctive in cross-section, with a central area of mostly small, thick-walled cells that is surrounded by looser tissue, followed again by small, thick-walled cells in the outer cortical region.

Tomenthypnum nitens

Plants robust, with numerous erect-spreading leaves that give the plant a stiff appearance. Leaves lanceolate, narrowly acuminate, strongly plicate. Costa rather weak, extending well above mid-leaf but often hard to see because of plications. Cells linear except at base.

Warnstorfia exannulata

Leaves almost straight to falcate-secund, ovate-lanceolate and narrowly acuminate, the costa extending into the acumen. Leaf margins serrulate, at least towards apex. Leaf cells linear, except at base. Alar cells hyaline and inflated,

extending almost to the costa (may remain attached to stems if leaves are broken off or removed). Stems with an outer layer of small cells; central strand present.

(c) Vascular plant remains

dicot leaves

Leaves or fragments of leaves with reticulate venation, except for those that can be assigned to the category 'ericaceous leaves'.

Equisetum

Herbaceous fragments that are reddish-brown to black; often shiny. Roots with longitudinal striations. Epidermal cells of larger fragments long, rectangular, arranged in ± regular rows. Walls between adjacent cells strongly sinuose.

ericaceous leaves

Leaves or fragments of leaves with reticulate venation that can be assigned to ericaceous taxa. If found close to the surface, these resemble fresh leaves of the various species. In more decomposed material, robust leaves or fragments with coriaceous texture, revolute margin, or dense tomentum. Borderline cases were assigned to the more general category 'dicot leaves'.

ericaceous roots

Fine woody roots, reddish to dark brown. Branching irregular, with slight triangular thickenings at branching points. Root tips not markedly rounded or swollen;

herbaceous

A very broad category that includes vegetative remains (both above- and belowground) of herbaceous taxa (excluding *Equisetum*).

Larix needles (*L. laricina*)

Elongate fragments, often reddish-brown, with a mottled appearance along the margins; darker and slightly raised in the centre. Flat to narrowly oval in cross-section; usually < 0.7 mm wide.

Picea needles

Short or elongate fragments, mid to dark brown, often with several rows of stomata apparent on either side of a central raised axis. Fresh material is rhomboidal or triangular-rhomboidal (ca. 1.3 x 1.0 mm) in cross section. In more decomposed specimens, tissue on either side of the central bundle may collapse.

robust woody roots

Coarse woody roots with rounded, sometimes markedly swollen tips. Branching is variable, but the clearest examples of this root type have short, lateral shoots that arise at ± right angles from a straight central axis. Most tree and non-ericaceous shrub species that grow in peatlands of western Canada (*P. mariana, L. laricina, Salix* and *Betula* spp) are likely to have roots that fall into this category.

smooth woody roots

Brown roots, irregularly branched, that resemble robust woody roots but lack the characteristic rounded or swollen tips of that category.

wood / bark

A very broad category that includes wood and bark as well as woody twigs and rhizomes.

(d) other

charcoal

Black fragments with a metallic lustre that crumble when probed with a dissecting needle or fine forceps.

APPENDIX 3

Macrofossil diagrams for Athabasca cores 3, 10, 16, 17 and 18

On each diagram, the vertical axis represents sample depth, with frequencies (%) of different macrofossil taxa plotted on the horizontal axes. Occurrences at frequencies <1% are marked by a plus sign (+). Stippled horizontal lines, where present, mark boundaries between stratigraphic zones identified by constrained cluster analysis. Zones are numbered at the right margin of each diagram.

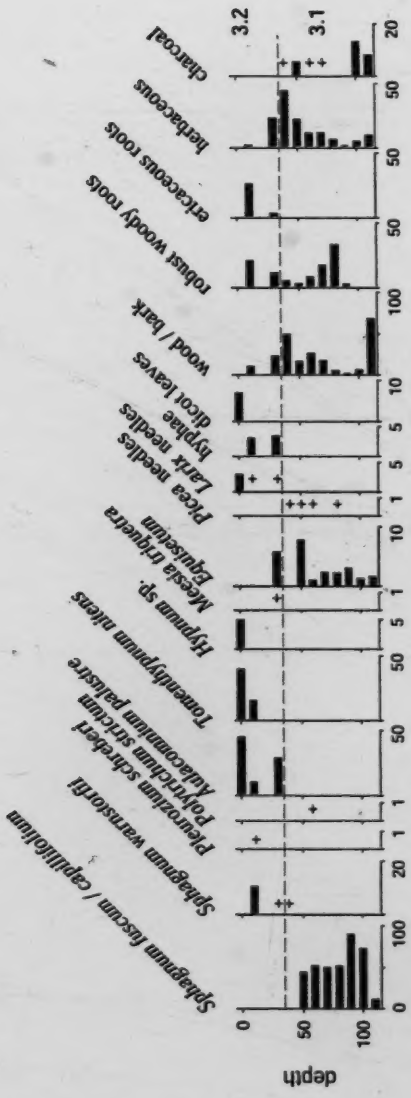


Figure A3.1: Macrofossil diagram for Athabasca core 3 (fen edge)

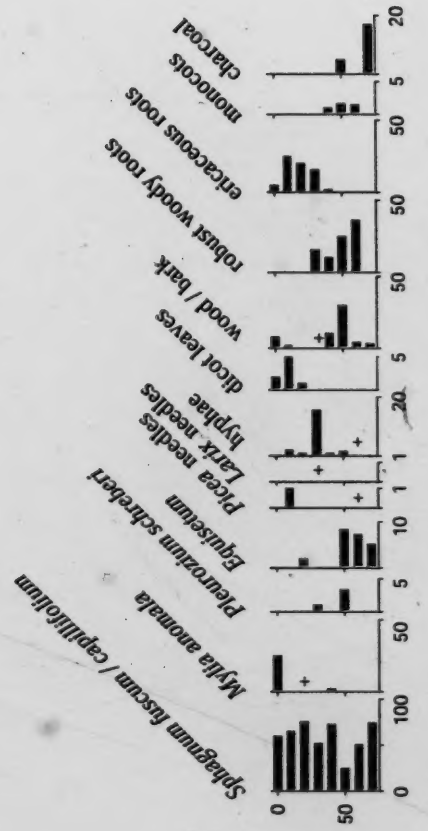


Figure A3.2: Macrofossil diagram for Athabasca core 10 (western bog)

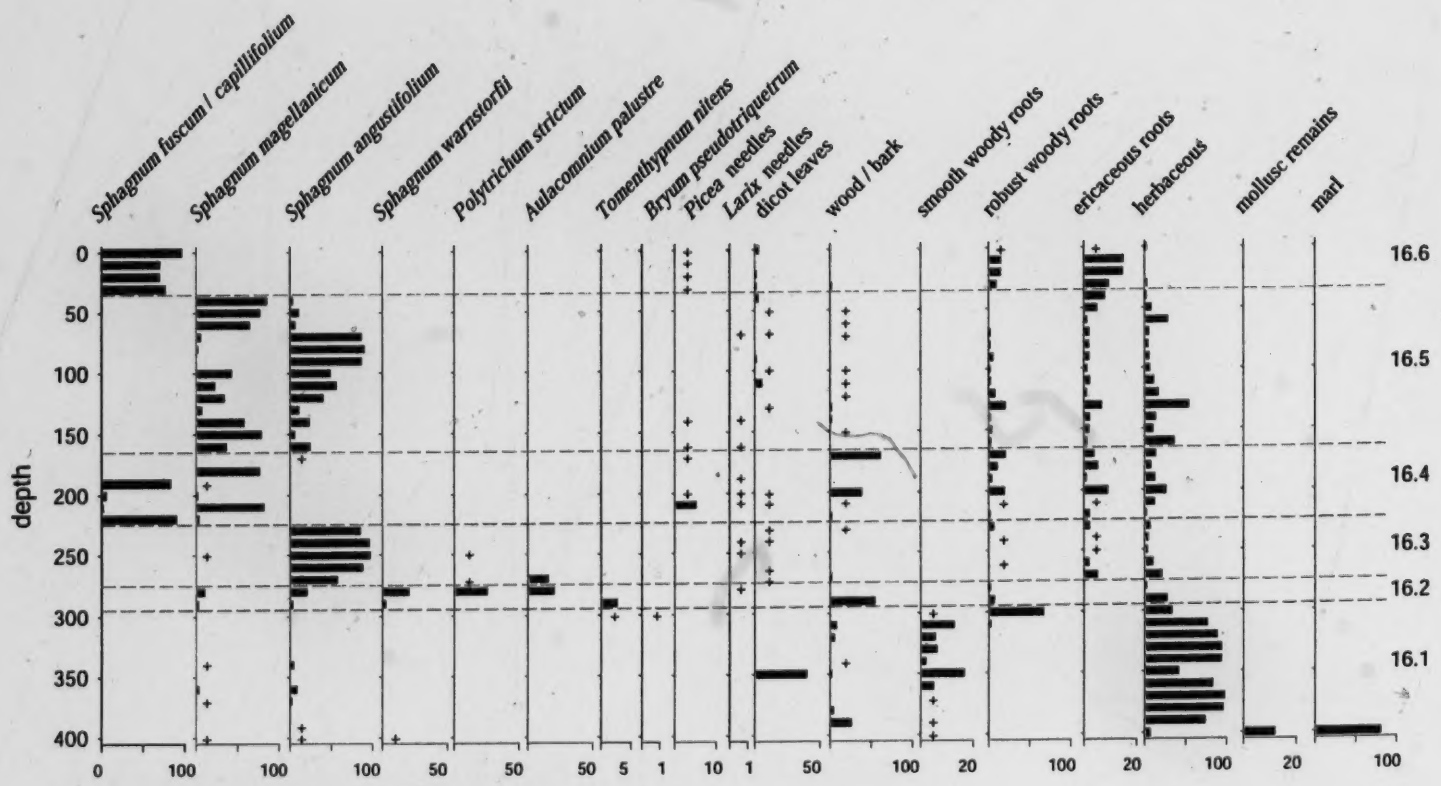


Figure A3.3: Macrofossil diagram for Athabasca core 16 (northern bog)

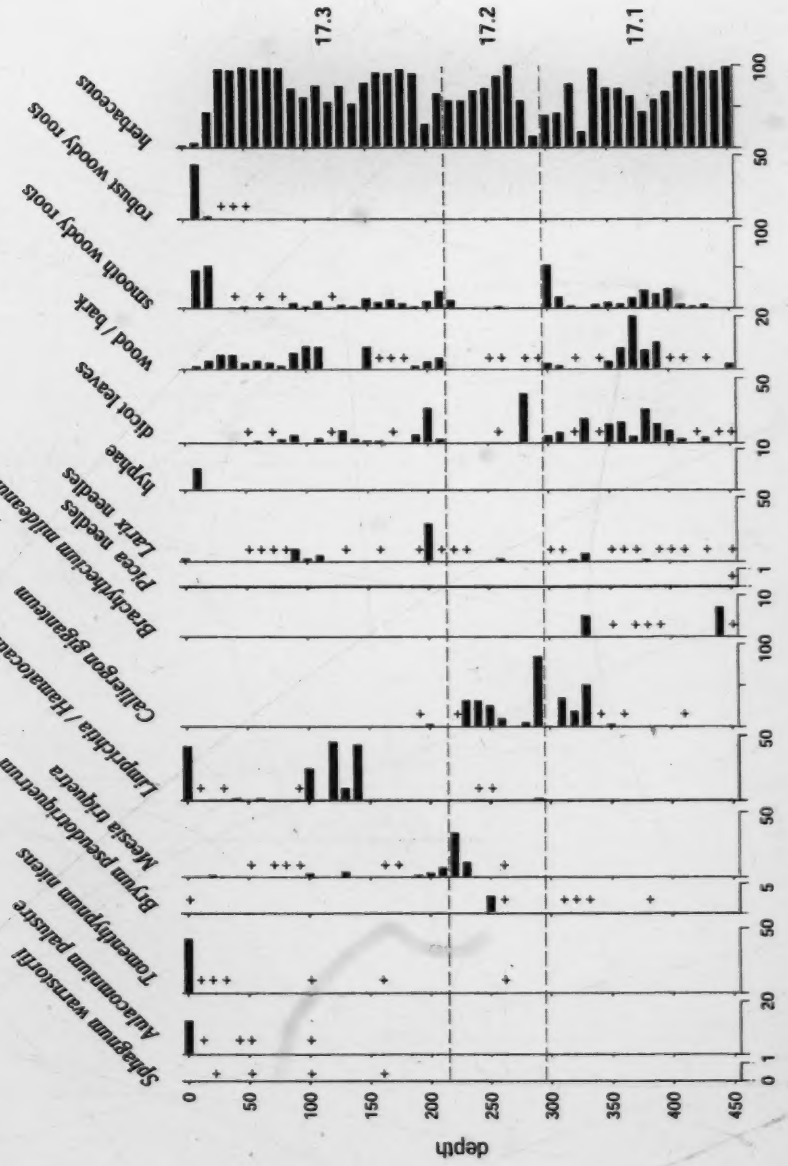


Figure A3.4: Macrofossil diagram for Athabasca core 17 (open fen)

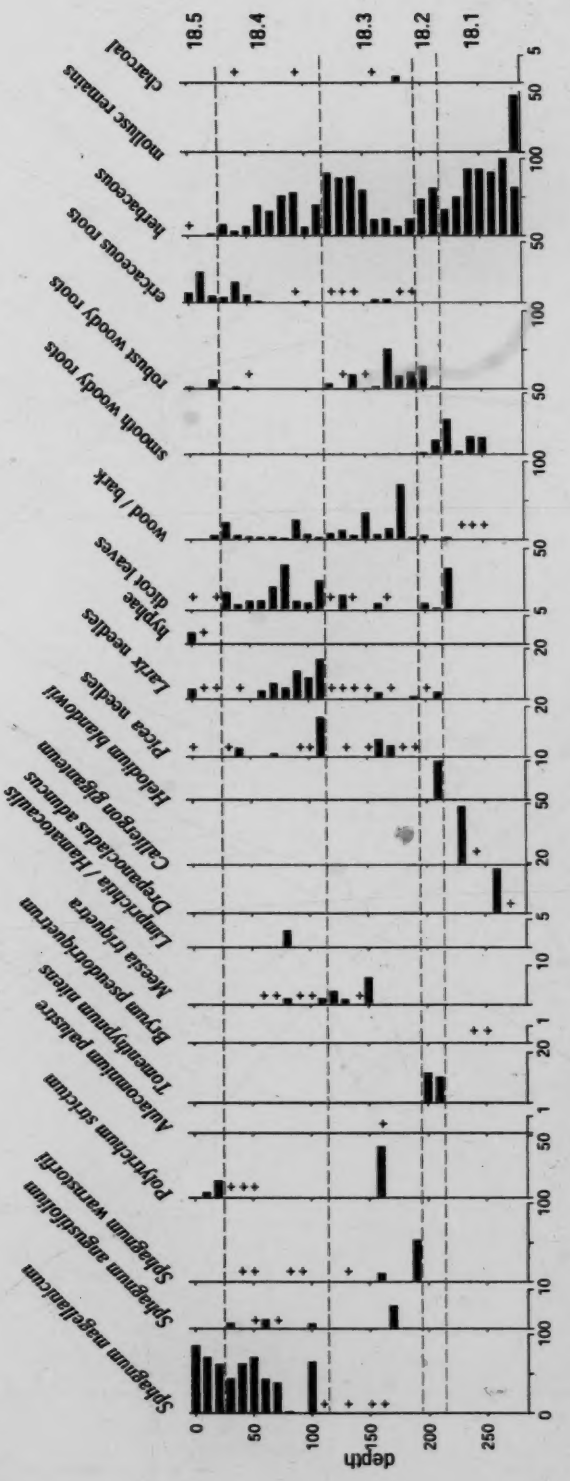


Figure A3.5: Macrofossil diagram for Athabasca core 18 (treed fen)